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Population Dynamics of the Peruvian scallop *Argopecten purpuratus* during the El Niño Phenomenon of 1983

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Wolff, M. 1987. Population dynamics of the Peruvian scallop *Argopecten purpuratus* during the El Niño phenomenon of 1983. Can. J. Fish. Aquat. Sci. 44: 1684–1691.

Population size, growth, and mortality rates of the Peruvian scallop (*Argopecten purpuratus* were studied during the El Niño event of 1983 in the fishing area off Pisco, Peru. Gonadal index and larval abundance of this scallop as well as measurements of in situ temperature, dissolved oxygen, and plankton volumes were taken to record spawning activity and environmental conditions. The scallop population size exceeded 60 times that of "normal" years. It is thought to be due to a significant increase in survival rate of larval and juvenile scallops and/or intensified spawning activity with subsequent recruitment in the warm El Niño waters. Only small scallops (15–45mm shell height) showed accelerated growth due to elevated temperatures. Total mortality (*Z*) was estimated as 2.5 and natural mortality (*M*) as 1.0. the hypothesis is proposed that *A. purpuratus* is a relict of a tropical/subtropical fauna inhabiting the Peruvian and Chilean waters in the Miocene, which has maintained its warmwater characteristics during evolution in the cold upwelling water because of periodic post-Miocene El Niño events.

On a étudié, au cours du El Niño de 1983, la taille des effectifs, la croissance et les taux de mortalité du pétoncle péruvien (*Argopecten purpuratus*) exploité par la pêche effectuée au large de Pisco, au Pérou. On a recueilli des données sur l'indice gonadique et l'abondance des larves de pétoncles et déterminé *in situ* la température, l'oxygène dissous et les volumes du plancton comme indices de l'activité reproductrice et des conditions environnementales. La taille des effectifs était 60 fois supérieure à celle observée au cours des années «normales». Selon l'auteur, cela résulte d'une augmentation importante du taux de survie des larves et des juvéniles et/ou d'une activité reproductrice intensifiée suivie d'un recrutement dans les eaux chaudes du El Niño. Seuls les petits pétoncles (hauteur de coquille de 15 à 45mm) ont montré un taux accéléré de croissance on régime de température élevée. On a déterminé que la mortalité totale (*Z*) et la mortalité naturelle (*M*) s'élevaient respectivement à 2,5 et 1,0. L'auteur formule l'hypothèse que *A. purpuratus* est une espèce relique d'une faune tropicale ou subtropicale qui peuplait les eaux péruviennes et chiliennes au cours du Miocène et qui a gardé ses caractéristiques d'espèce d'eau chaude au cours de son évolution dans les eaux froides des remontées à cause de la présence périodique, après le Miocène, du El Niño.

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The fishing area off Pisco lies about 250 km south of Lima (between 14°20′S and 13°35′S) and is influenced by a nearby upswelling center. For decades, it has been the most important area for Peruvian invertebrate fisheries, in particular for scallops and mussels (Wolff and Wolff 1983; Wolff 1984). Since the beginning of spring 1982, an abnormal increase in water temperature was recorded in the area of Pisco. In January 1983, temperature in the shallow bays reached 28–29°C, 6–8° higher than in normal years. As a consequence, many fish and invertebrate species adapted to cool, upwelling waters, died, or migrated (Arntz and Valdivia 1985). Surprisingly, this was not true for scallops; divers reported a massive occurrence of juvenile scallops on the beds in February 1983.

The present investigation studied population size, growth rates, and mortality rates of this scallop, *Argopecten purpuratus*, as affected by the unusual El Niño conditions; data taken during a subsequent "normal" year, as well as data from a previous, study (Wolff and Wolff 1983) are included for comparative purposes.

Material and Methods

Environmental Parameters and Plankton Analysis

Temperature was measured at the experimental site (Fig. 1) at weekly intervals between 0900 and 1100 by a handheld thermometer 1 cm off the bottom. At the same time, water was taken just above the bottom for oxygen measurements by the Winkler method.

For weekly plankton samples a net of 2.5-m length, 0.2-m diameter, and a mesh size of 80 μm was used. It was pulled a distance of 200 m (marked by two floats) horizontally in midwater about 1.5 m below the surface at a velocity of approximately 45 $m \cdot min^{-1}$. The plankton was fixed in 5%

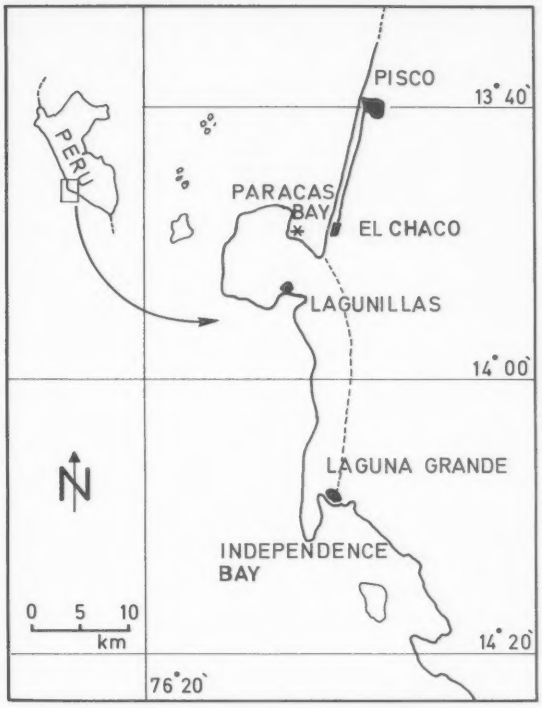

FIG 1. Pisco fishing area and experimental site.

formalin and subsequently analysed as follows: filtration through an 80-μm sieve to determine the net volume, filtration through a 200-μm sieve to separate the two fractions (80 and 200-μm), and resuspension of the two plankton fractions and a count of the scallop larvae in a 1-mL subsample using a binocular microscope at 40 times magnification.

The total number of scallop larvae was calculated by multiplying the subsample counts by the original plankton volume. To express the larval density in seawater, the volume of water filtered was calculated by multiplying the distance the net was pulled by the net area.

Gonad Index Analysis, Measurements of Size–Weight Relations

Weekly samples of 30 adult individuals were taken at the experimental site (Fig. 1). At this sample size, the standard error of the mean gonad index remained below 5%, which was regarded as sufficiently precise. The following relationship was used to determine the gonad index (GI):

$$GI = (\text{fresh wet weight of gonad/fresh wet weight of soft parts}) \times 100.$$

To calculate the relations between shell size and the weights of the muscle and the soft parts, the following relationship was used:

$$W = a \cdot H^b$$

where W = wet weight (grams) and H = shell height (millimetres)

Population Size

The Peruvian scallop fishery is of a pulsed nature, as the annual catch depends completely on the strength of recruitment at the beginning of the year. Population size at the start of the fishing season can therefore be estimated using cumulative fishing success methods, like the one of Leslie (1952), which only requires data on catch and effort. Some simplifying assumptions have to be made, however, when this method is used: catchability remains constant during the fishing period, there is no significant recruitment, and immigration or emmigration and natural mortality is negligible. Only the latter factor seemed to be a problem here, as the fishery lasted over a period of 7 mo and natural mortality is high in this fast-growing species. The author therefore attempted to modify Leslie's formula incorporating the instant rate of natural mortality (M) (Wolff 1987). The modified version consists of the following linear regression:

$$(C_t/f_t)/(e^{-M_t}) = qN_o - qK_t e^{0.5M_t}$$

where C_t = catch in interval t (in numbers), f_t = effort in interval t, q = coefficient of catchability, N_o = initial stock size (numbers), K_t = cumulative catch (= half of catch in interval t plus sum of previous catches), and M = instantaneous rate of natural mortality. As can be seen from the equation, the catchability coefficient q is calculated from the slope b and initial population size N_o from the y-intercept.

Growth

Three independent methods were used to determine the growth parameters of the scallop: interpretation of length frequencies, a tagging experiment, and growth observation in off-bottom cages.

Interpretation of length frequencies

Within a period of 1 yr (May 1983 to May 1984), every 3 wk a sample was taken by scuba diving over a 15-min period on a scallop bed at the experimental site (Fig. 1), and all scallops seen were collected. The size frequencies of the catches were analysed using a computer program termed ELEFAN I (Pauly and David 1980). This program allows for a reliable estimation of the growth parameters without knowing the individual age of the animals. To detect oscillations in the growth rate during the annual cycle, Pauly and Gaschuetz (1979) incorporated the following extended version of the von Bertalanffy growth equation in the program:

$$L_t = L_\infty\,(1\text{-}e^{-k[(t\text{-}t_o) + C/2 \sin 2\,(t\text{-}t_s)]}$$

where L_t, L_∞, t_o, and k = growth parameters of the von Bertalanffy growth equation, C = constant, which represents the amplitude of growth oscillation, and t_s = starting point of oscillation with respect $t_o = 0$.

Tagging experiment

On the same scallop bed at the experimental site (Fig. 1), a total of 319 scallops between 18 and 85 mm shell height were collected and released after being tagged with a numbered plastic mark attached with epoxy cement to the upper valve. During the tagging process, the scallops were exposed to air for approximately 20 min before being returned to the water. the growth parameters were obtained using the Gulland and Holt (1959) plot:

$$L_2\text{–}L_1/(t_2\text{–}t_1) = a - b\bar{L}$$

TABLE 1. Catch and effort data of the scallop fishery during the period August 1983 to February 1984 (the fourth and fifth column contain the values used for the plot of Fig. 3).

	f_t (boats)	C_t (10^6 ind.)	$\frac{C_t}{f_t} \cdot \frac{1}{e^{-M_t}}$	$K_t \cdot e^{0.5M_t}$ (10^6 ind.)
1983				
August	70	36.96	573885.34	19.29926
September	100	47.52	561382.47	65.99681
October	170	62.83	474575.79	131.32737
November	300	95.04	492130.62	230.16681
December	250	52.80	320368.60	331.00131
1984				
January	200	36.96	304683.69	426.44024
February	100	13.10	236544.24	478.15747

where L_1 and L_2 = length of scallop corresponding to time t_2 and t_1 and $\bar{L} = L_1 + L_2)/2$. The growth parameter k is calculated by $k = -b$ and the parameter L_∞ by $L_\infty = a/k$.

Growth experiment in off-bottom cages

Four movable cages (Fig. 2) were installed in a bottom culture of scallops inshore from the scallop bed of the experimental site (Fig. 1). The cages were filled with four different size groups of scallops in order to obtain growth rates for each size group. Every 2 wk the scallops were measured to the nearest millimetre using a caliper and the mortality was registered. Before being returned to the water, the cages were cleaned of mud and algae; the scallops were exposed for approximately 30 min to air during this procedure.

After drawing the growth curves for the various size groups in the cages, the growth constant k was obtained for each interval between two measurements using a plot developed by Munro (1982):

$$\log (L_\infty - L_1) - \log (L_\infty - L_2) = k (t_2 - t_1).$$

The k values obtained for each interval were then plotted against in situ temperature, oxygen, gonad index, and plankton volume in the corresponding interval to evaluate the effect of these parameters on the growth rate of the scallop.

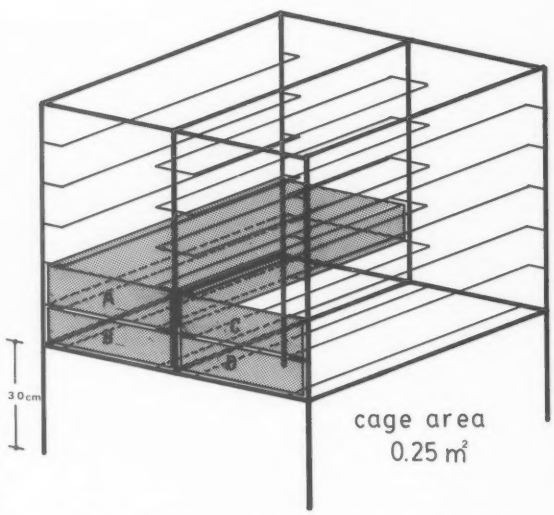

FIG. 2. Off-bottom cages for the scallop growth experiment.

Mortality Rates

Natural and fishing mortality were estimated by a linear regression method developed by Paloheimo (1961) of the following form:

$$\ln (C_t/C_t + 1) = q + 0.5 (f_t + f_{t+1}) + M,$$

An independent estimate for natural mortality (M) was obtained using an empirical formula (Pauly 1980). It was assumed, however, that M would be overestimated by this formula, since it does not consider alterations in natural mortality due to biotic alterations as produced during the El Niño event, which may have affected survival rates of the scallops.

Results

Population Size

Figure 3 shows the regression calculated with the modified version of Leslie's formula using the data of Table 1. The calculated initial population size in numbers can be expressed in biomass, as an estimate of average scallop size at the beginning of the fishing season. The following size–weight relationships were also available:

$$\text{Shell weight} = 2.92 \cdot 10^{-4} \cdot H^{2.8}$$

$$\text{Weight of soft parts} = 1.30 \cdot 10^{-5} \cdot H^{3.4}$$

$$\text{Weight of adductor muscle} = 1.09 \cdot 10^{-5} \cdot H^{3.26},$$

where H = shell height (millimetres). The average shell height at the beginning of the season was estimated as 70 mm, corresponding to a total weight of approximately 67 g. Multiplied by the initial stock number (811 413 180), a stock biomass of 54 365 t was calculated at the beginning of the fishing season.

Growth

Length frequencies

The original length frequencies used as input data for the ELEFAN I program are shown in Fig. 4. The growth parameters

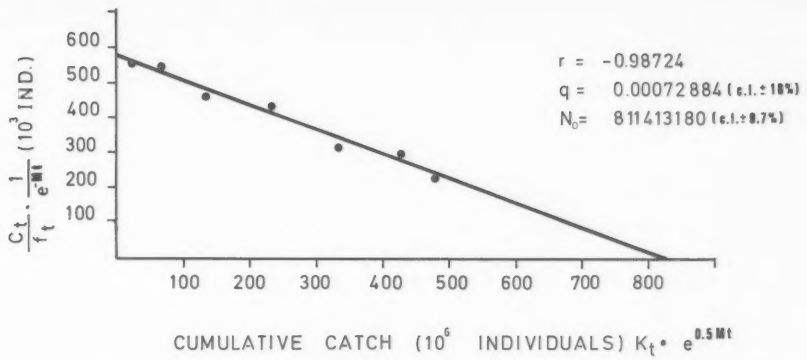

FIG. 3. Modified version of Leslie's plot for population size and catchability estimates (data of Table 1).

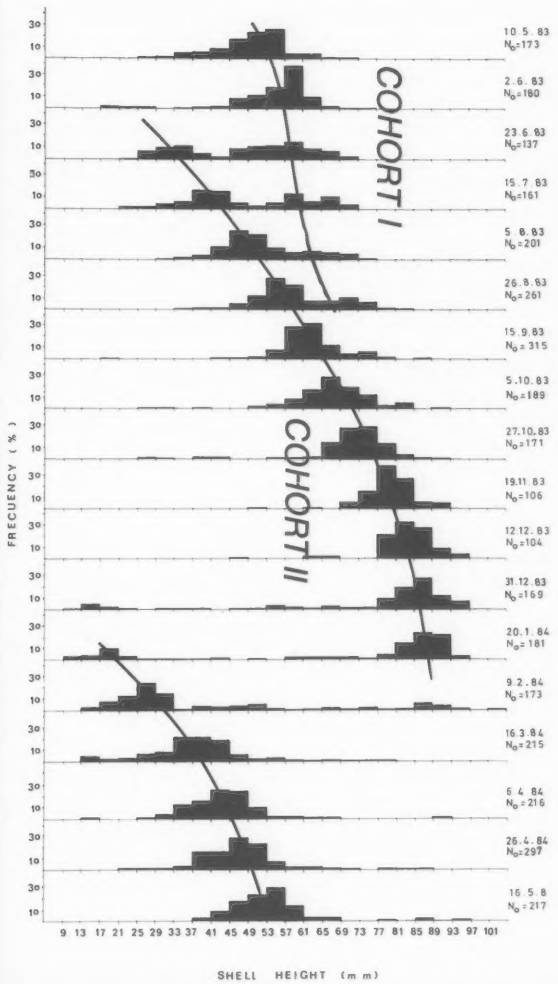

FIG. 4. Length frequencies of 18 *A. purpuratus* catches taken at the experimental site (see Fig. 1).

of the two distinguishable cohorts were as follows:

	L_∞ (mm)	k	C	W_p	ESP/ASP
Cohort I (spring born)	110	1.26	0.2	0.5	0.499
Cohort II (autumn born)	111.5	2.10	0	0	0.814

where ESP/ASP is a measure of the fit of the growth curve (range 0–1) (see Pauly and David 1980)

Tagging experiment

The Gulland and Holt plot established with the data from the recaptured individuals is shown in Fig. 5. As can be seen from the distribution of the points around the regression line, the variability of individual growth is high resulting in wide confidence limits for the parameters k and L_∞. All recaptured individuals were found within the area of approximately 100 m from the station where they had been released, indicating that significant migration had not taken place.

Growth in off-bottom cages

The growth for each size group in the different cages is shown in Fig. 6. The cohort in cage C grew almost without any seasonal oscillation whereas the scallops in cages A and B exhibited a pronounced decrease in growth rate during autumn and winter. The cohort in cage D grew slower until reaching a size of about 45 mm; thereafter, growth was comparable with the cohort in cage C. For the cohort in cage B (spring born) and cage C (late summer, autumn born), the following growth parameters were calculated: Cohort B: $k = 2.02$, $L_\infty = 95$; cohort C: $k = 2.68$, $L_\infty = 95$. For these two cohorts the following relative growth rates were calculated (initial size 35.6 mm): cohort B: 62.6% in 108-d period from April to July; cohort C: 96.6% in 108-d period from June to October. The calculated k values of cohort B for each growth interval (e.g. between two measurements) in relation to environmental parameters are shown in Fig. 7.

Mortality

The regression line calculated by Paloheimo's formula using the data of Table 1 is shown in Fig. 8. As the fit with the original monthly data was not good ($r = 0.36$), the data were pooled and two monthly averages calculated which resulted in a significant

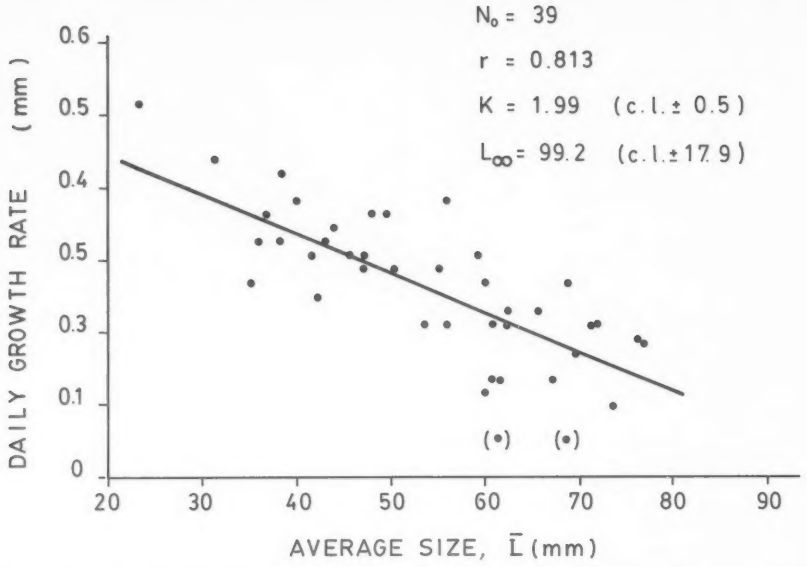

FIG. 5. Gulland and Holt (1959) plot used for growth parameter estimates from tagged and recaptured scallops.

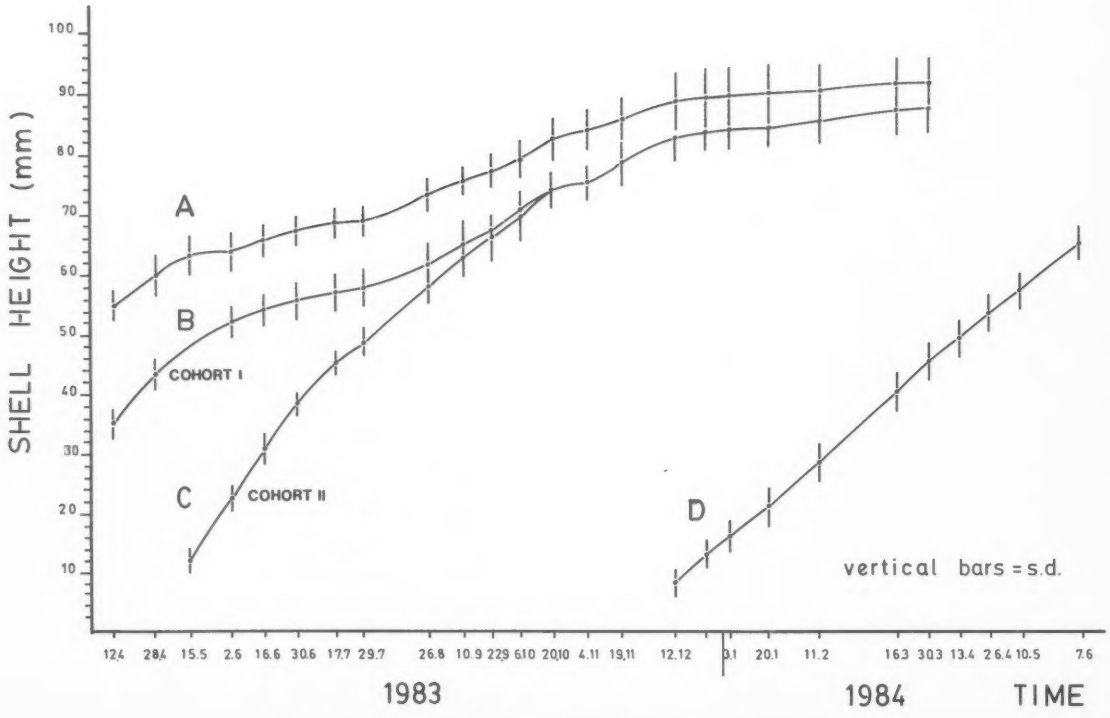

FIG. 6. Growth of scallops of four different size groups in off-bottom cages.

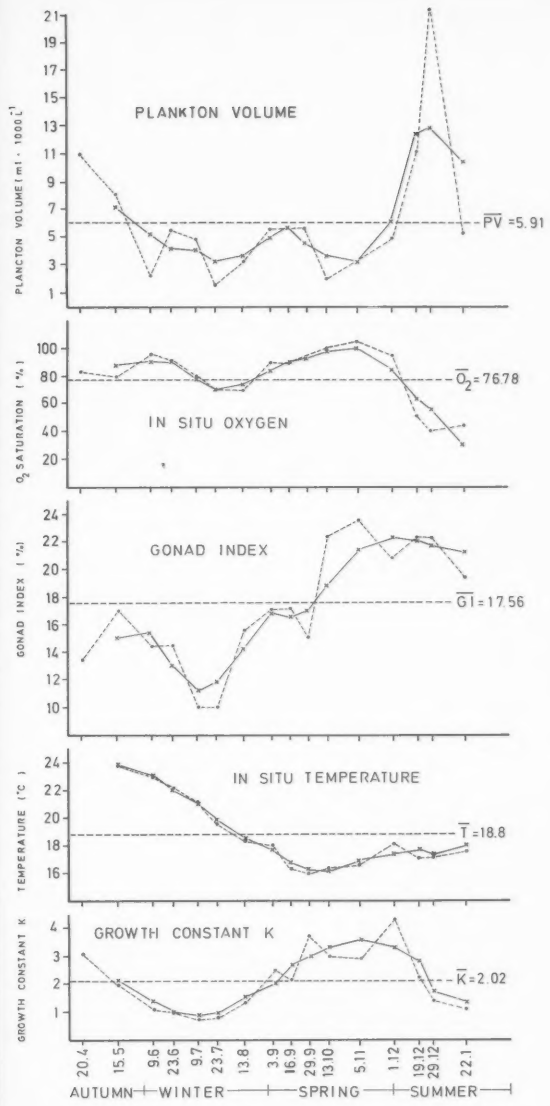

FIG. 7. Measurements taken at the experimental site (see Fig. 1) (broken line: original data; solid line: moving average over three data points); *k* values for scallops of cage B (cohort I, see Fig. 6).

improvement of the fit ($r = 0.95$). Since this method allows for the estimation of catchability q, mean fishing mortality during the fishing period can be estimated as $F = q$ mean effort. Since mean monthly effort was estimated as 170 boats, fishing mortality was calculated as $0.1257 \cdot ms^{-1}$ or $1.5 \cdot yr^{-1}$. Natural mortality (M) was calculated as $0.0846 \cdot mo^{-1}$ or $1.0 \cdot yr^{-1}$. To calculate M independently, the growth curve parameters derived from the length frequency analysis (program ELEFAN I) an a mean annual temperature of 19°C were inserted in Pauly's formula:

$$\log M = -0.0066 - 0.2791 \log L_\infty + 0.65431 \log k + 0.46341 \log T$$

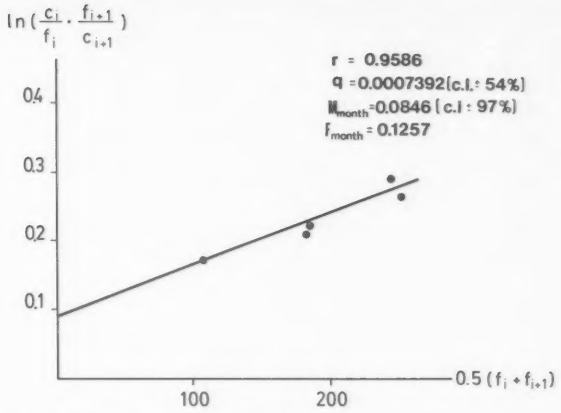

FIG. 8. Paloheimo's linear regression used for estimates of natural mortality (data of Table 1).

M (cohort I) = 3.1

M (cohort II) = 2.3

Mean population $\bar{M} \approx 2.7$.

The lower and upper confidence limits of the growth parameters obtained from the tagging experiment (Fig. 5) were also inserted in the above formula resulting in M values of 2.5 (lowest) and 3.9 (highest).

Discussion

Population Size/Biomass

The total catch (about 23 000 t) and the stock size estimated at the beginning of the fishing season of over 50 000 t were higher than ever recorded in the history of the scallop fishery in the Pisco area and resulted in the construction of numerous commercial processing plants. The total area where the fishery was concentrated was estimated as between 628 and 942 ha, thus giving an estimate of mean density of 86–129 scallops$\cdot m^{-2}$. This value coincides with personal diving observations and corresponds to a scallop biomass of 5.3–8 kg$\cdot m^{-2}$. This is comparable with maximum biomasses in the shallow-water bottom cultures of this species in the Bay of Paracas (Fig. 1).

In the 10-yr period before El Niño in 1983, *A. purpuratus* contributed only about 10% of the total catch of molluscs in the area (MIPE 1972–82); the remainder was provided by the mussel *Aulacomya ater* (approximately 50%), the clam *Gari solida* (approximately 11%), the snail *Thais chocolata* (approximately 18%), and others (approximately 11%). The total annual catch of invertebrates including crustacean species was approximately 10 000 – 12 000 t, less than half of the *A. purpuratus* catch in 1983. This means that although a high number of commercially important invertebrate species died or migrated during the impact of El Niño of 1983, the total catch was more than doubled due to the population explosion of the scallop. In terms of economic yield, the gain from the scallop fishery was even higher.

Growth

The present study provides four main results: (1) the stock consists of two distinguishable cohorts with different seasonal

patterns of growth, (2) acceleration of growth in relation to high El Niño temperatures could be detected only for small, probably immature scallops (10–45 mm), (3) growth in cages above the seafloor is faster than on the seafloor, and (4) individual growth differs considerably on the sea bottom.

Seasonal decrease in growth rate was only found for the spring-hatched cohort I after spawning in late summer/autumn (Fig. 6). The relative growth rate during the subsequent 3-mo period was 62.6% compared with 96.6% for same sized scallops of cohort II during the winter months. Figure 7 shows that growth rate of cohort I (expressed here as growth coefficient k) is correlated with the gonad index; e.g. it is low when gonad index is low (autumn, winter) and increases when the gonad index increases (spring, summer). The growth rate of this cohort seems negatively correlated with in situ temperature.

By contrast, cohort II (hatched in late summer/autumn) grew rapidly during the late autumn and winter months and reached a size equal to that of cohort I within 6 mo. This cohort probably did not spawn until late spring/early summer and thus used a major part of available energy for growth, since cohort I spawned in the autumn and a significant proportion of its available energy must have been used for maturation and spawning leading to a subsequent decrease in growth in winter. It thus appears that higher water temperatures led to an acceleration of growth in smaller, premature individuals whereas adults responded with an increase in reproductive activity.

It is interesting to note that in Chile, *A. purpuratus* was recently transferred from Coquimbo (30°S) to Chiloe (43°S) which lies about 500 km south of the southern limit of its natural distribution, and preliminary results (A. Sanhueza, pers. comm.) indicate that it adapts well and that its growth rate is comparable with that in Coquimbo despite lower water temperatures. *Argopecten purpuratus* is apparently able to adapt to different and frequently changing environments. In cold periods (in the Peruvian upwelling system usually related to upwelling periods), feeding and growth conditions are presumably good whereas offspring production is probably low. Under these conditions, adult growth may compensate for natural mortality. In contrast, during warm periods, juvenile growth and offspring production are favoured, leading to rapid population increases. With these characteristics, added to its early maturity, its hermaphroditism, and its high fecundity of about 200 million eggs·yr^{-1} (M. Wolff, unpubl. data), *A. purpuratus* is a typical *r*-selected species (MacArthur and Wilson 1967).

The results of the tagging experiment indicated that individual growth rates differ considerably among the scallops on the seabed, probably due to microscale differences in the environmental conditions and not to genetic differences, since growth in the off-bottom cages was more homogeneous.

Faster growth in the cages can probably be attributed to a better supply of food and oxygen above the sea bottom. However, the difference in growth rate compared with the scallops on the seabed was small, which is remarkable when the high densities of approximately 100 scallops·m^{-2} on the seabed are considered.

Mortality

If the two estimated values for M (using Paloheimo's regression method and Pauly's empirical formula) are compared, the difference ($2.7 - 1.0 = 1.7$) is remarkable. It should be noted, however, that the precision of the M value calculated by Paloheimo's regression is low, as indicated by the wide confidence limits (Fig. 8). Assuming, however, that Pauly's formula gives an M estimate that is representative for "normal conditions" and also assuming that the M value obtained by Paloheimo's method reflects the natural mortality during the El Niño in 1983, it is just this difference that explains (at least in part) the population explosion of the scallop.

The local crab (*Cancer* spp.), known as the main predator of the scallops, died or migrated at the beginning of the El Niño event (Arntz and Valdivia 1985) and was only partially replaced by octopus (*Octopus*. spp.). Competition for space and food was reduced significantly, since most of the other filter feeders of quantitative importance in the area (such as the mussel *A. ater*) also died. In addition, two other factors probably contributed to the scallop population explosion: (1) A much faster development of the larvae in the warm El Niño water. DiSalvo et al. (1984) found in laboratory experiments that larvae grown at 25°C reached metamorphosis much earlier than larvae grown at 19°C and the survival rate was considerably higher in the warmer water. It is reasonable to assume that under natural conditions, larval survival is increased even more when the larval period is shortened, since the time the larvae are exposed to predators and strong currents that could carry them out of the area is reduced.

(2) The high level of oxygen saturation on the scallop beds detected during the El Niño warming (see Fig. 7). Usually the warming of the water is accompanied by a decrease of oxygen concentration over the scallop beds, thus causing occasional mass mortalities of the scallop during the summer months. During the El Niño impact, however, oxygen levels remained high even during the warmest months of the year, enabling an enormous number of scallop larvae to settle and survive.

The increased temperatures might have also favoured phytoplankters suitable for feeding and assimilation by the scallops.

The study shows that *A. purpuratus* not only resisted the unusually high water temperatures during El Niño of 1983, but was apparently favoured by them. Until now, this scallop has been described as a typical coldwater species of the Peruvian/Chilean coast adapted to the upwelling conditions (Olsson 1961). This description does not agree with the observations made during the El Niño of 1983. Waller (1969) studied the evolution within the Argopecten group using fossil records. He found its origin to be in the tropical/subtropical waters of the Caribbean and Atlantic. Before the Panamanian land bridge was formed, a part of this group emigrated into the Pacific where it subsequently gave rise to a few species, of which two — *Argopecten circularis* (the present dominant pectinid of the Panamanian fauna) and *A. purpuratus* (the present pectinid of the Peruvian and Chilean coast) — still exist. Zinsmeister (1978) studied the fossil mollusc fauna of central Chile and found that subtropical conditions prevailed in the southeast Pacific during the middle and late Miocene. Afterwards the climate cooled off and the subtropical fauna was replaced by a subantarctic one, which predominates the Chilean waters of today.

The results of the present study, together with the findings of Waller (1969) an Zinsmeister (1978), suggest that *A. purpuratus* is a relict form of a subtropical fauna that once existed in Chile and Peru. Such a history would agree better with its high temperature resistance/preference under the El Niño impact of 1983. It is possible that such temperature resistance/preference would be lost during evolution in the cold upwelling water if it were not of an adaptive advantage. It is reasonable to infer that previous El Niño's have probably occurred frequently

enough, subsequent to the general cooling of the water in the late Miocene, to preserve the warm-water characteristics of this species.

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Analysis of Planktonic Rotifer Assemblages from Sudbury, Ontario, Area Lakes of Varying Chemical Composition

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Planktonic rotifer samples were collected from 47 Sudbury, Ontario, area lakes to determine factors influential to species distributions. The lakes ranged from highly acidic and metal contaminated to circumneutral with low metal concentrations. Median rotifer abundance was substantially higher in non-acid (pH > 5.2) than in acid (pH < 5.2) lakes, although differences in species distributions were evident. Application of detrended correspondence analysis to rotifer species densities revealed broad separation of communities from acid and non-acid lakes. Assemblages from acid lakes were highly similar in species composition and dominance, while those from non-acid lakes were generally much more heterogeneous. It was hypothesized that planktonic rotifer communities converged in species composition as a consequence of the stress of lake acidification, in a pattern similar to that previously described for planktonic crustaceans. Among the best predictors of rotifer community composition were lake pH and the concentrations of manganese and aluminum.

On a prélevé des échantillons de rotifères planctoniques dans 47 lacs de la région de Sudbury (Ontario) afin de déterminer les facteurs qui influent sur la répartition des espèces. Les eaux des lacs allaient de très acides et contaminées par des métaux à presque neutres avec de faibles concentrations de métaux. L'abondance médiane des rotifères était nettement plus élevée dans les lacs non acides (pH > 5,2) que dans les lacs acides (pH < 5,2) et des différences entre les répartitions spécifiques étaient évidentes. Une analyse factorielle de correspondance des densités des espèces de rotifères a révélé un important écart entre les communautés des lacs acides et non acides. Les assemblages des lacs acides étaient très semblables pour ce qui est de la composition et de la dominance spécifique tandis que, dans les lacs non acides, ils étaient généralement beaucoup plus hétérogènes. On formule l'hypothèse que les communautés de rotifères planctoniques ont fait l'objet d'une convergence touchant leur composition spécifique suite au stress de l'acidification lacustre et cela selon un régime semblable à celui décrit précédemment pour les crustacés planctoniques. Parmi les meilleures variables explicatives de la composition de la communauté des rotifères, ou compte le pH lacustre et les concentrations de manganèse et d'aluminum.

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Acidic precipitation is widely recognized as having adversely affected terrestrial and aquatic ecosystems in western Europe and eastern North America. In Canada, the Sudbury, Ontario, region has received considerable scientific attention since Gorham and Gordon (1960) first described chemical modifications of surface waters resulting from very large local smelter emissions.

Among the most intensively studied groups of biota in acid lakes are the zooplankton (Sprules 1975; Roff and Kwiatkowski 1977; Yan and Strus 1980; Malley et al. 1982; Keller and Pitblado 1984). Crustacean zooplankton diversity in acidic, metal-contaminated Ontario lakes is often impoverished relative to that in non-acidic lakes of similar morphometry. For example, in the La Cloche Mountains 60 km southwest of Sudbury, Sprules (1975) observed that crustacean zooplankton diversity was reduced in acid lakes, with the most acidic lakes containing only one species (*Diaptomus minutus*).

Rotifers may act as better indicators of exogenous stresses on plankton communities than crustaceans, since their diversity, abundance, and fertility frequently exceed comparable values

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for crustaceans (Allen 1976; Roff and Kwiatkowski 1977; Gilbert 1985). Hydrogen ion concentration has long been considered to be an important determinant of rotifer community composition (see review in Pennak 1978), although several workers (Edmondson 1944; Hutchinson 1967) have cautioned that species distributions may be influenced by other chemical factors, especially by CO_2, HCO_3^-, Ca, and mineral salts. Siegfried et al. (1984) and Carter et al. (1986) observed that rotifer community composition in Adirondack Mountain lakes and New Brunswick – Nova Scotia lakes was related to pH and other related factors.

The relationship between lake acidity and total rotifer density is less clear. Synoptic studies have revealed that attendant with increased lake acidity, total abundance may increase (Malley et al. 1982; Schindler et al. 1985; Yan and Geiling 1985), decrease (Roff and Kwiatkowski 1977; Carter et al. 1986), or appear unaffected (Siegfried et al. 1984).

In this study we examine the planktonic rotifer communities from northeastern Ontario lakes of varying chemical composition in an attempt to determine factors governing species distributions. Additionally, we test the hypothesis that total rotifer abundance does not differ between acid and non-acid lakes.

Methods

Forty-seven lakes located within 175 km of Sudbury were selected for the study. Many of the lakes have been previously investigated by the Ontario Ministry of the Environment (MOE) (Keller and Pitblado 1984) and have been identified as having been affected by smelter emissions. The lakes are located primarily to the northeast and southwest of Sudbury along the prevailing wind directions.

Collections for chemical and zooplankton analyses were made between 16 July and 7 August 1984 from a central location in each lake. Access to 39 lakes was by fixed-wing aircraft, while the remaining 8 lakes were sampled by boat. Samples for chemical analysis were collected by immersing a tygon tube from the surface to the lower limit of the metalimnion (MOE 1979). All total inflection point (TIP) alkalinity and pH measurements were made using a Radiometer PHM 64 pH meter, while conductivity was determined and corrected to 25°C by a Radiometer CDM3 conductivity meter. Two protocols were followed in other chemical analyses. Briefly, for the 39 lakes sampled by floatplane, one sample for analysis of Mn, Al, Zn, Cu, Ni, Pb, and Fe was preserved with 0.5 mL of Analar-grade nitric acid for subsequent determination by atomic absorption spectroscopy (MOE 1981). A second sample was used for determination of Ca, Mg, K, Na, SO_4^{2-}, Cl, and SiO_3. Complete methods are outlined in MOE (1981). For the remaining eight lakes, concentrations of Mn, Al, Zn, Cu, Ni, Pb, Fe, Mg, Ca, and total S were determined using inductive coupled plasma (ICP) emission spectroscopy at the University of Toronto. A comparison of chemical methods is given in the Appendix. In general, there was good agreement between the methods, although in some instances ICP sulphur values were considerably lower than the sulphate values obtained using the first method (ion chromatography). Values for Na, K, Cl, and SiO_3 were obtained from 1983 data, as 1984 values were unavailable, while 1981 total P values were used for all lakes (W. Keller, unpubl. data).

Zooplankton samples were collected by a vertical haul from 1 m above bottom to the lake surface using a metered 44-μm Wisconsin-style net with a 12.5-cm-diameter mouth. Samples were preserved in a 5% sugar–formalin solution and later enumerated as subsamples following settling in sedimentation tubes for a minimum of 3 h. In general, a minimum of 300 individuals was counted per subsample, with additional subsamples being examined for rare species. All densities were corrected for filtration efficiency. The presence or absence of *Leptodora kindtii* and *Chaoborus* spp. was simply noted, since quantitative determinations of these organisms are difficult to make when collections are made during daylight hours.

Statistical Analysis

Chemical differences between acid ($pH < 5.20$; $N = 31$) and non-acid ($pH > 5.20$; $N = 16$) lake groups were examined with Student's *t*-tests, while differences in rotifer diversity and density were investigated using Mann–Whitney *U*-tests. Variability in community composition was analyzed using species densities and detrended correspondence analysis (DCA). DCA is an ordination procedure which allows for the projection of a multidimensional data swarm in low-dimensional space (Gauch 1982). Samples (lakes) with similar patterns of species composition and dominance have similar "loadings" or positions on DCA plots. DCA is generally considered to be superior to earlier ordination techniques because it "detrends" data, thereby preventing artificial "arch effects" and because it rescales each axis to uniform subdivision length (Gauch 1982).

Canonical correlation analysis was then used to explore the relationship between the DCA results (criterion set) and lake physical–chemical parameters (predictor set). The analysis was repeated using biotic variables (crustacean zooplankton species densities, *Leptodora* and *Chaoborus* presence/absence) as the predictor set. Between variable sets, canonical correlation coefficients (R^2) represent the variability of one set explained by the other. The significance of the correlations was tested using the *F*-test of Miller (1975).

Results

A large proportion (>65%) of the lakes had pH values below 5.2 and alkalinity values below 20 $\mu eq \cdot L^{-1}$ (Fig. 1a). While the concentrations of Al, Mn, and Zn were significantly higher ($p < 0.05$) in acid than in non-acid lakes (Fig. 1b, 1c, 1d), concentrations of Cu and Ni were not significantly different ($p > 0.05$; Fig. 1e, 1f). Acid lakes contained significantly higher ($p < 0.03$) levels of sulphate than non-acid lakes (Fig. 1g) and lower concentrations of Ca, Mg, and K ($p < 0.001$; Fig. 1h, 1i, 1j). Acid lakes were also more transparent ($p < 0.03$) and generally had lower total P values (Fig. 1k and 1l, respectively).

Thirty-seven rotifer species occurred in two or more lakes in the study (Table 1). The median number of species was significantly higher ($p < 0.001$) in non-acid (14.5) than in acid (8.0) lakes, despite the fact that sample depth was greater for the latter group (Table 2). Median rotifer density was significantly higher ($p < 0.05$) in non-acid (140.6 ind.$\cdot L^{-1}$) than in acid (67.2 ind.$\cdot L^{-1}$) lakes. However, a multiple regression model indicated that total P concentration was a better predictor of total rotifer density and that the effect of pH was indirect (Table 3).

The most frequently encountered species were *Gastropus* spp., *Keratella taurocephala*, *K. cochlearis*, *Polyarthra vulgaris*, and *Trichocerca multicrinis* (Table 1). Each of these species, excepting *T. multicrinis*, was dominant (>10% of total

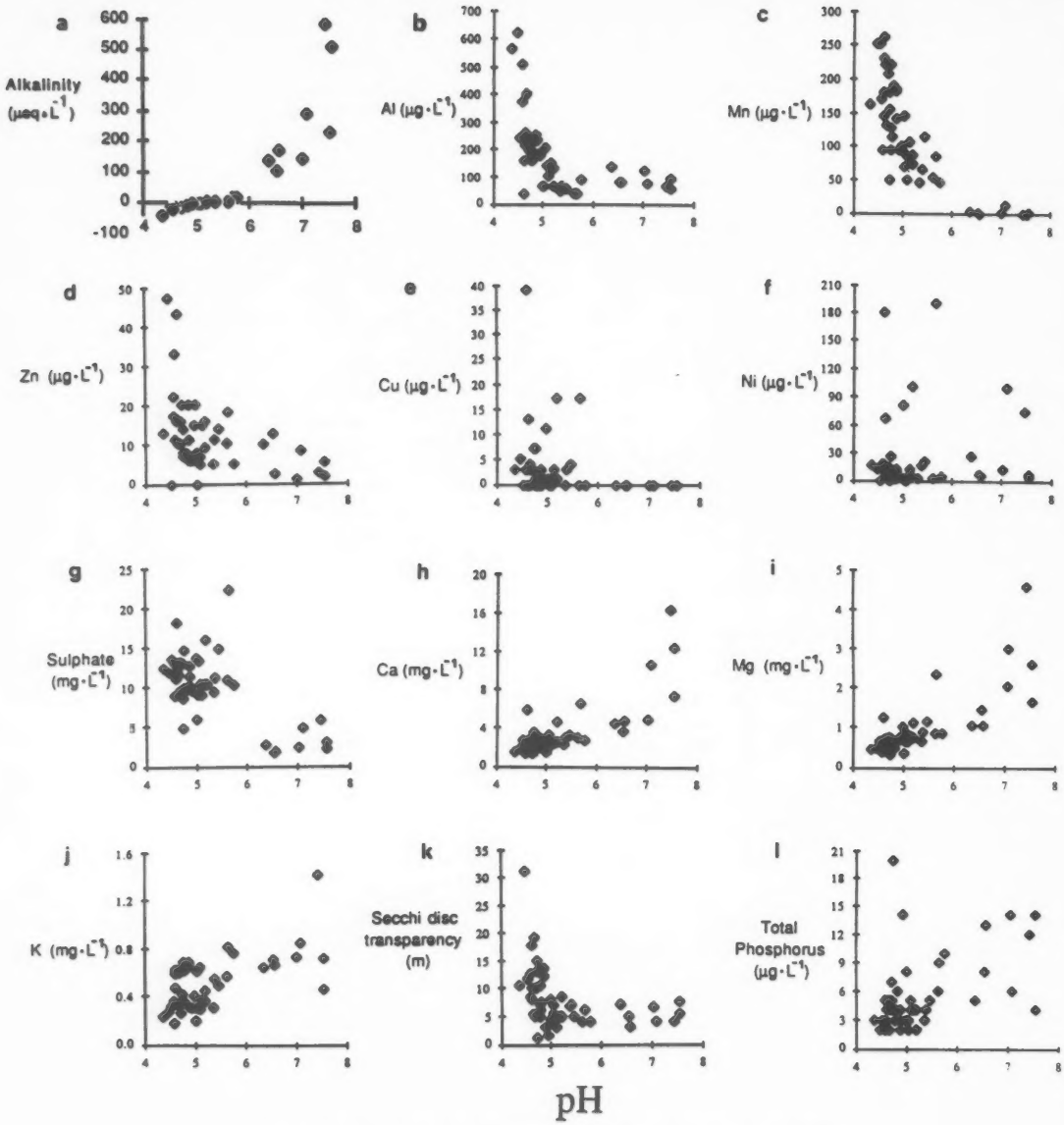

FIG. 1. Relationships between physical–chemical parameters and lake pH.

rotifer abundance) in more than 25% of the lakes. The relative abundance of many species appeared to be pH dependent; *K. taurocephala* and *Gastropus* together accounted for >70% of the total rotifer abundance in acidic lakes and <5% in non-acid lakes. In some acid lakes, *K. taurocephala* so dominated the rotifer fauna that the densities of all the other species combined accounted for <5% of total abundance. The dramatic decline in the abundance of *K. taurocephala* began at about pH 4.8, with the species being virtually absent from lakes with pH > 6.0 (Fig. 2).

While the overall distribution of *K. cochlearis* was nearly a mirror image of that for *K. taurocephala* (Fig. 2), its density in individual lakes was not correlated (Pearson's $r = -0.13$) with that of *K. taurocephala*. *Keratella cochlearis* was rarely found below pH 5.3, but it was a dominant member of the community in 88% of lakes with pH > 5.5. *Keratella cochlearis* and *P. vulgaris* together accounted for only 3.1% of total rotifer density in acid lakes and 75.9% in non-acid lakes. *Polyarthra vulgaris* and *P. remata* were frequently encountered species in the study (62 and 39% of lakes, respectively; Table 1). Both species were more abundant in non-acid than in acid lakes, and neither species occurred in lakes with pH < 4.5. Similarly, the predatory rotifer *Asplanchna priodonta* and its larger congener *A. herricki* occurred primarily in near-neutral lakes, although

TABLE 1. Occurrence and dominance of 37 rotifer species in the study lakes

Species	Occurrence		% of lakes in which dominant (>10%)
	Number of lakes	% of lakes	
Ascomorpha ecaudis	4	8.5	2.1
A. saltans	2	4.3	0
A. ovalis	7	14.9	2.1
Asplanchna priodonta	20	42.6	2.1
A. herricki	3	6.4	0
Conochilus unicornis	17	36.2	8.5
C. hippocrepis	2	4.3	2.1
Conochiloides natans	13	27.7	8.5
Euchlanis pellucida	2	4.3	2.1
Gastropus spp.	47	100	51.1
Kellicottia bostoniensis	14	29.8	4.3
K. longispina	14	29.8	2.1
Keratella cochlearis	31	66.0	25.5
K. crassa	20	42.6	2.1
K. earlinae	7	14.9	0
K. hiemalis	8	17.0	0
K. taurocephala	41	87.2	68.1
Lecane flexilis	3	6.4	0
L. mira	12	25.5	0
Lepadella acuminata	4	8.5	0
L. ovalis	4	8.5	0
Monostyla closterocerca	2	4.3	0
M. copeis	2	4.3	0
M. lunaris	14	29.8	0
M. obtusa	2	4.3	0
Ploesoma truncatum	19	40.4	0
Polyarthra major	7	14.9	2.1
P. remata	17	36.2	4.3
P. vulgaris	29	61.7	38.3
Synchaeta spp.	26	55.3	4.3
Testudinella parva	3	6.4	0
Trichocerca cylindrica	8	17.0	0
T. multicrinis	31	66.0	0
T. porcellus	3	6.4	0
T. rousseleti	3	6.4	0
T. similis	10	21.2	0
Trichocerca spp.	4	8.5	0

the distribution of *A. priodonta* extended into mildly acid waters.

DCA results are presented in Fig. 3 for the two primary axes of the species density ordination. These axes accounted for 47 and 27%, respectively, of the total variability in the ordination (Table 4). The grouping of the lakes along the axes of the figure (Fig. 3a) indicate that rotifer communities in acid lakes were relatively homogeneous in comparison with communities in circumneutral lakes. Specifically, acid lake communities characteristically were dominated by only a few species, most notably *K. taurocephala* and *Gastropus*, while non-acid lakes were dominated by a larger array of species, including *K. cochlearis*.

Application of canonical correlation analysis to DCA results demonstrated that chemical factors correlated best with DCA axis 1, while biological parameters (i.e. crustacean predictors) correlated most strongly with DCA axis 2. For example, canonical variate 1 (CV 1) of the physical–chemical data set was significantly correlated ($r = -0.921$; $p < 0.01$) with DCA axis 1 (Table 5). Negative correlations with CV 1 indicate that

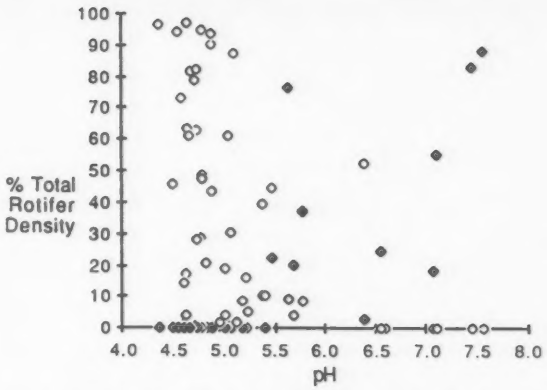

FIG. 2. Percent composition of the total rotifer density for *Keratella taurocephala* (◇) and *K. cochlearis* (◆) as a function of lake pH.

values for physical–chemical parameters increase with increasing DCA scores on axis 1. The best correlates of CV 1 included pH (Fig. 3a), Mn concentration (Fig. 3b), alkalinity (Fig. 3c), and Mg and Ca (Fig. 3d) concentrations (Table 5). Other physical–chemical variables which correlated with CV 1 included the concentrations of total P, K, and Al (Table 5). No significant correlations were observed between any other canonical variates for the physical–chemical data and the DCA axes.

While the greatest amount of variation in the ordination of rotifer communities is accounted for by physical–chemical variables, variation along DCA axis 2 correlated best with CV 1 for the biotic variables ($r = -0.891$, $P < 0.01$; Table 6). In general, correlations between original crustacean densities and their corresponding canonical variates (intraset correlations; Table 6) were lower than those observed between physical–chemical parameters and their canonical variates (Table 5), possibly because it is more difficult to accurately determine animal densities than chemical concentrations in water. The highest correlations with CV 1 were obtained with the densities of *Diaptomus oregonensis* and *Daphnia* spp. (Table 6). However, many of the correlations between crustacean densities and CV 1 are perhaps spurious, as densities of many crustacean and rotifer species covary as a function of lake pH. In addition, assigning biological significance to correlations between CV 1 of the crustacean data set and the DCA axes is made difficult by the fact that separation of lakes on DCA axis 2 occurred mainly with non-acid lakes (Fig. 3a), of which there were a limited number in the study.

Discussion

The acidification of freshwater ecosystems represents a major ecological problem. Recent investigations have demonstrated that many groups of organisms, including planktonic rotifer communities, are affected by acidification related phenomena (Schindler et al. 1985; Carter et al. 1986, and references therein; MacIsaac et al. 1986). In the current study, median rotifer diversity decreased from 14.5 species in non-acid lakes to 8.0 species in acid waters. This finding corresponds well with results from previous studies in both Europe (Almer et al. 1974) and eastern North America (Roff and Kwiatkowski 1977; Bradt et al. 1984; Siegfried et al. 1984; Carter et al. 1986).

TABLE 2. Summary statistics for physical–chemical parameters of the study lakes.

Parameter	Lake group: pH < 5.2 (31 lakes) Mean	Lake group: pH > 5.2 (16 lakes) Mean	*t*-statistic	$p <$
pH[a]	4.76	5.71	10.3	0.001
Alkalinity ($\mu eq \cdot L^{-1}$)	−15	136	4.6	0.001
Specific conductance ($\mu S \cdot cm^{-1}$)	37.5	71.6	3.2	0.003
Secchi disc transparency (m)	9.1	5.5	2.3	0.025
Mg ($mg \cdot L^{-1}$)	0.6	1.6	5.1	0.001
Ca ($mg \cdot L^{-1}$)	2.4	5.8	4.5	0.001
K ($mg \cdot L^{-1}$)	0.3	0.6	5.3	0.001
Na ($mg \cdot L^{-1}$)	0.7	3.3	2.6	0.012
Al ($\mu g \cdot L^{-1}$)	232.3	75.3	4.6	0.001
Mn ($\mu g \cdot L^{-1}$)	150.6	36.6	6.9	0.001
Zn ($\mu g \cdot L^{-1}$)	14.1	8.2	2.1	0.044
Fe ($\mu g \cdot L^{-1}$)	93.2	67.1	0.9	0.395
Cu ($\mu g \cdot L^{-1}$)	3.8	2.6	0.6	0.575
Ni ($\mu g \cdot L^{-1}$)	17.8	35.9	1.4	0.168
SO_4^{2-} ($mg \cdot L^{-1}$)	11.1	8.0	2.4	0.021
Cl ($mg \cdot L^{-1}$)	0.5	5.3	2.4	0.019
SiO_3 ($mg \cdot L^{-1}$)	0.9	1.3	1.0	0.331
Total P ($\mu g \cdot L^{-1}$)	4.7	6.6	1.6	0.112
Lake area (ha)	319	350	0.28	0.778
Lake depth (m)	21.0	20.0	0.2	0.839
Sample depth (m)	18.6	8.9	3.5	0.001
Distance from Sudbury (km)	72.4	41.2	3.1	0.003

[a]Based on $[H^+]$ equivalents.

TABLE 3. Multiple regression analysis of total rotifer densities on lake pH and total P concentration for the survey lakes.

Source	df	SS	MS	*F* value	Pr > *F*
Model	3	464 177	154 726	9.69	0.0001
Error	43	686 517	15 966		
Total	46	1 150 694			

Source	df	Type 3	*F* value	Pr > *F*
pH	1	26 878	1.68	0.2014
phosphorus	1	65 114	4.08	0.0497
pH*phosphorus	1	117 626	7.37	0.0095

The effect of lake acidification on overall rotifer abundance is less clear. While our finding of decreased abundance in acid lakes agrees with the results of Roff and Kwiatkowski (1977), Brezonik et al. (1984), and Carter et al. (1986), they contrast with those of Yan and Miller (1984) and Schindler et al. (1985). Siegfried et al. (1984) found that clear, acid Adirondack lakes supported low rotifer populations, while humic, acid lakes supported higher densities. These disparate results may be reconciled in some instances by considering the productivity of the lakes involved (Carter et al. 1986) and the extent to which they have been contaminated by heavy metals. In the current study, total rotifer density correlated better with total P concentration than with the concentration of heavy metals and lake pH, indicating that lake productivity may well have been the primary determinant of total rotifer density.

Although overall rotifer density declined at low pH, species differences were evident. The predominant species in acid lakes included *K. taurocephala* and *Gastropus*. *Keratella taurocephala* has been observed in acid lakes over much of eastern North America (Roff and Kwiatkowski 1977; Malley et al. 1982; Bradt et al. 1984; Chengalath et al. 1984; Siegfried et al. 1984; Yan and Miller 1984; Carter et al. 1986). The species appears highly adapted to life in acid lakes since its large anterolateral spines may render it invulnerable to predation by invertebrates (e.g. *Chaoborus*; Moore and Gilbert 1987) which commonly occur in fishless acid lakes (MacIsaac 1986). Moreover, its body morphology minimizes sinking, and as a consequence, the energy expenditure required to remain in the plankton (R. S. Stemberger, Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, pers. comm.). As a result, *K. taurocephala* is able to live in relatively unproductive waters, such as those which might result as a consequencr of lake acidification where the total amount of edible phytoplankton is low (Havens and DeCosta 1985; Schindler et al. 1985; Stokes and Yung 1986).

Very little is currently understood regarding the factors which determine the distribution of *K. taurocephala* in relation to lake chemistry. Yan and Geiling (1985) and MacIsaac et al. (1986) reported large populations of *K. taurocephala* in an acidic (pH = 4.0) lake (Swan) located near Sudbury. However, it was not found in any acidic (pH < 4.0) ponds at the Smoking Hills, N.W.T., nor in Silver Lake, another highly acidic (pH = 4.1) Sudbury lake (H. MacIsaac, unpubl. data). The dominant species in both of these systems was *Brachionus urceolaris*, a species previously reported in highly acidic volcanic lakes in Japan (Masiko 1938) and in acid mine drainage lakes in Indiana (Smith and Frey 1971) and Missouri (Campbell et al. 1964). While the absence of *K. taurocephala* from the

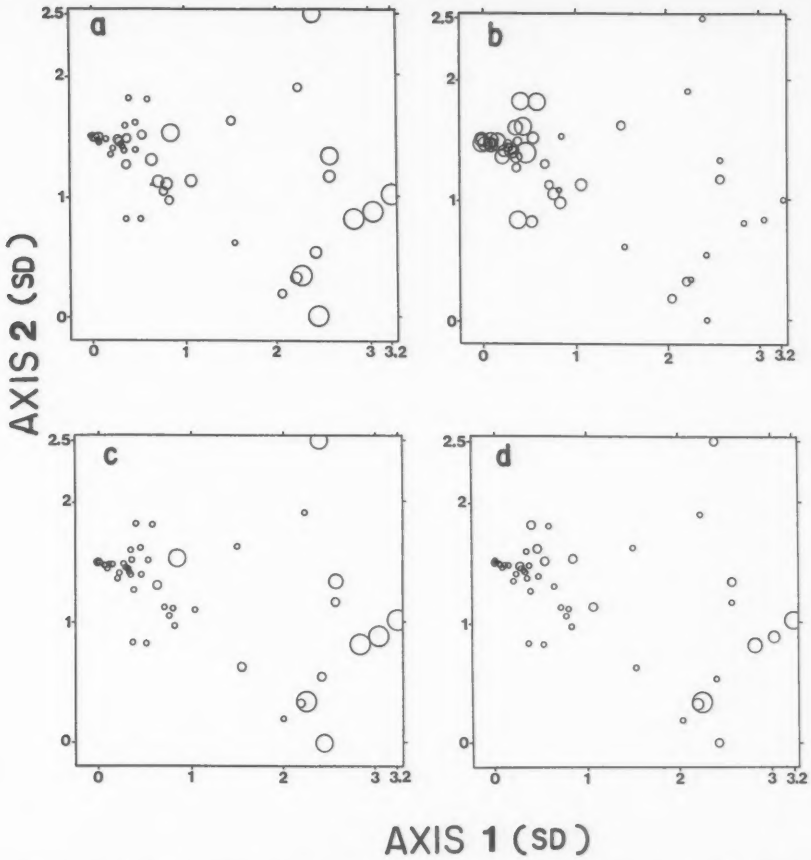

FIG. 3. Variability (standard deviations) in rotifer communities as determined by a detrended correspondence analysis model based on species densities (see text for further explanation). For each of the following, parameter value increases with circle: (a) pH, (b) total MN concentration, (c) TIP alkalinity, (d) Ca concentration. Maximum values: pH = 7.58, Mn = 260 $\mu g \cdot L^{-1}$, alkalinity = 585 $\mu eq \cdot L^{-1}$, Ca = 16.4 $mg \cdot L^{-1}$; minimum values: pH = 4.39, Mn ≤ 0.1 $\mu g \cdot L^{-1}$, alkalinity = −32 $\mu eq \cdot L^{-1}$, Ca = 1.3 $mg \cdot L^{-1}$.

TABLE 4. Species lists for rotifers that loaded most heavily onto the two primary DCA axes. Species at the high end of axis 1 are characteristic of non-acid lakes, while those at the low end are more characteristic of acidic waters. The middle 17 species (not shown) are considered nonpreferential. Beside each axis is the proportion of total variability in the ordination accounted for by that axis.

Axis 1 (47%)		Axis 2 (27%)	
Highest scores	Lowest scores	Highest scores	Lowest scores
Keratella cochlearis	*Trichocerca porcellus*	*Keratella earlinae*	*Asplanchna herricki*
Monostyla closterocerca	*Monostyla obtusa*	*Conochilus unicornis*	*Asplanchna priodonta*
Trichocerca rousseleti	*Keratella taurocephala*	*Ascomorpha ovalis*	*Ascomorpha ecaudis*
Conochilus hippocrepis	*Synchaeta* spp.	*Monostyla closterocerca*	*Ploesoma truncatum*
Asplanchna herricki	*Gastropus* spp.	*Euchlanis pellucida*	*Keratella crassa*
Keratella earlinae	*Ascomorpha saltans*	*Lecane flexilis*	*Polyarthra remata*
Trichocerca cylindrica	*Keratella hiemalis*	*Lepadella ovalis*	*Keratella hiemalis*
Kellicottia longispina	*Lepadella acuminata*	*Conochilus hippocrepis*	*Kellicottia longispina*
Keratella crassa	*Conochiloides natans*	*Trichocerca rousseleti*	*Polyarthra vulgaris*
Asplanchna priodonta	*Testudinella parva*	*Kellicottia bostoniensis*	*Lepadella acuminata*

TABLE 5. Loadings of physical–chemical variables on three canonical variates of the predictor set where rotifer DCA axes represent the criteria. Parenthetical numbers (canonical correlation coefficients) represent the amount of variation in the DCA axes explained by the canonical variates of the physical–chemical data set.

Variable	CV 1	CV 2	CV 3
Criteria (interset correlations)			
DCA axis 1	−0.921 (0.848)	0.162 (0.026)	0.126 (0.016)
DCA axis 2	0.563 (0.317)	−0.133 (0.018)	0.434 (0.188)
DCA axis 3	0.234 (0.055)	0.680 (0.462)	0.399 (0.159)
Predictors (intraset correlations)			
pH	−0.864.	0.066	0.133
Alkalinity	−0.698	−0.016	0.127
Mg	−0.685	0.019	−0.011
Ca	−0.664	−0.129	0.108
K	−0.570	0.162	−0.029
Na	−0.406	0.141	−0.158
Specific conductance	−0.487	0.001	−0.046
Mn	0.740	−0.234	0.012
Al	0.559	0.027	0.140
Zn	0.344	0.043	0.069
Cu	0.153	−0.329	−0.080
Ni	−0.143	−0.249	−0.049
Total P	−0.594	0.233	0.107
SO_4	0.462	−0.303	−0.166
Colour (Hazen)	−0.265	0.436	0.315
Secchi disc transparency	0.452	−0.038	0.107
Lake area	−0.165	0.172	0.030
Sample depth	0.393	0.033	−0.306
Lake depth	0.207	0.068	−0.211
Distance from Sudbury	0.202	0.081	−0.159

arctic ponds may be related to difficulties in dispersal, it is more difficult to explain its absence from Silver Lake, as the species occurs in many nearby lakes. Silver Lake and many of the arctic ponds are contaminated with extremely high levels of Al, Mn, Zn, Ni, and Cu (W. Keller, unpubl. data; Havas and Hutchinson 1983). In comparison, Swan Lake and the lakes in this survey have lower levels of heavy metal contamination (MacIsaac 1986; MacIsaac et al. 1986). Thus, the distribution of *K. taurocephala* may well be restricted at low pH by direct or indirect effects of toxic concentrations of heavy metals, rather than by hydrogen ion toxicity. Community composition may be expected to shift from *K. taurocephala* dominated *B. urceolaris* dominated when concentrations of heavy metals and hydrogen ion are greatly elevated.

The contribution to total rotifer density by *K. taurocephala* was very low in lakes with pH values > 5.5 (Fig. 3). A similar pattern has also been demonstrated with Adirondack Mountain lakes by Siegfried et al. (1984). Since metal levels are generally low in circumneutral waters, it is unlikely that metal toxicity affected the distribution of *K. taurocephala* in our near-neutral study lakes. It is also unlikely that predation had any direct effect on *K. taurocephala* abundance in these lakes; low densities of the species were frequently accompanied by higher densities of similar-sized members of the genus (*K. earlinae*, *K. crassa*, and *K. cochlearis*).

Two alternative hypotheses which may account for the decline in importance of *K. taurocephala* at high pH are competitive interactions and physiological intolerance. Although the evidence necessary to test the hypotheses is scant, competitive interactions between rotifers and other zooplankton have been demonstrated. Cladoceran zooplankters may effectively suppress rotifer populations either by interference (Gilbert and Stemberger 1985) or exploitative competition (Neill 1984; Gilbert 1985; H. MacIsaac, unpubl. data). Moreover, since non-acid lakes frequently support larger populations of both rotifers and herbivorous crustacean zooplankton than comparable acid lakes (Roff and Kwiatkowski 1977; Brezonik et al. 1984), the potential for competitive interactions may be greater in non-acid lakes. However, recent attempts to culture *K. taurocephala* clones from softwater New England lakes in competition- and predation-free environments at pH > 6.0 have been unsuccessful (R. S. Stemberger, pers. comm.). Thus, the available evidence is consistent with the hypothesis of physiological intolerance to non-acid conditions rather than competitive exclusion.

The distribution of *K. cochlearis* in relation to lake acidity is also very poorly understood. The species was found almost exclusively in lakes with low heavy metal concentrations and pH > 5.5 in our study. These results agree with its distribution as reported by Siegfried et al. (1984) for Adirondack Mountain lakes and by Carter et al. (1986) for lakes in New Brunswick and Nova Scotia. Furthermore, both Roff and Kwiatkowski (1977) and Bradt et al. (1984) described higher densities of *K. cochlearis* in non-acid lakes in their surveys of both acid and non-acid lakes. By contrast, Malley et al. (1982) reported dramatic increases in the density of *K. cochlearis* in an experimentally acidified northwestern Ontario lake, while Brezonik et al. (1984) found the species in both acid and non-acid Florida lakes. These incongruous results may possibly be explained by assuming that different varieties, with different ecological tolerances, from the *K. cochlearis* species complex were involved.

TABLE 6. Loadings of crustacean and insect variables on three canonical variates of the predictor set where rotifer DCA axes represent the criteria. Parenthetical numbers (canonical correlation coefficients) represent the amount of variation in the DCA axes explained by the canonical variates of the crustacean and *Chaoborus* data set.

Variable	CV 1	CV 2	CV 3
Criteria (interset correlations)			
DCA axis 1	0.587 (0.345)	−0.489 (0.239)	−0.481 (0.231)
DCA axis 2	−0.891 (0.793)	−0.230 (0.053)	−0.070 (0.005)
DCA axis 3	−0.027 (0.001)	−0.466 (0.217)	0.345 (0.119)
Predictors (intraset correlations)			
Chydorus sphaericus	0.419	0.064	0.033
Daphnia galeata mendotae	0.495	−0.192	0.029
D. retrocurva	0.499	0.000	0.020
Diaphanosoma brachyurum	0.314	−0.032	0.054
Bosmina longirostris	−0.034	0.147	−0.163
Eubosmina spp.	−0.103	−0.536	0.032
Holopedium gibberum	−0.131	0.129	0.175
Polyphemus pediculus	−0.232	0.180	0.047
Leptodora kindtii	0.389	−0.322	−0.085
Diaptomus minutus	−0.103	0.253	−0.018
D. oregonensis	0.572	−0.023	0.091
D. sicilis	0.120	0.022	−0.563
Epischura lacustris	0.433	−0.163	−0.204
Senecella calanoides	0.348	−0.165	0.085
Calanoid copepodids	−0.292	0.286	0.270
Cyclops scutifer	0.139	−0.329	0.099
C. bicuspidatus thomasi	0.318	−0.438	0.050
C. vernalis	0.125	−0.568	0.255
Tropocyclops prasinus mexicanus	−0.208	−0.481	−0.318
Cyclopoid copepodids	0.171	−0.435	−0.273
Total nauplii	0.077	−0.591	−0.267
Chaoborus spp.	−0.030	0.033	0.255

Alternatively, the results of Malley et al. (1982) and Brezonik et al. (1984) indicate that heavy metals may also influence *K. cochlearis* distributions. Acidic lakes in both studies were low in metal contamination, yet they contained sizeable populations of *K. cochlearis*. Thus, it is conceivable that the distribution of *K. cochlearis*, as well as that of other species such as members of the genus *Polyarthra*, may well have been determined more by elevated levels of metals than by hydrogen ion toxicity.

Using multivariate statistical procedures, Carter et al. (1986) found that while Labrador and Newfoundland lakes lacked any distinct zooplankton community structure associated with acidification, structure in lakes in Nova Scotia and New Brunswick was significantly related to acidification-related factors. In Labrador, where acidification is negligible, zooplankton species were almost independently distributed. In contrast, lakes in Nova Scotia and New Brunswick which were located on granitic and dioritic rock formations around the Bay of Fundy displayed distinct community types. Rotifers associated with non-acid waters included *K. crassa*, *K. cochlearis*, *T. cylindrica* and *A. priodonta*, while *K. taurocephala* was the predominant species in acid lakes. These findings bear very close resemblance to our results for northeastern Ontario lakes. In both models the primary factor (axis) associated with community composition correlated best with pH, alkalinity, Ca, Mg, and Al. Our model also designated Mn as a strong correlate of DCA axis 1 and hence of rotifer community composition. Mn has also been identified as a potentially important determinant of other small-bodied zooplankton assemblages in Ontario lakes (Sprules and Knoechel 1984), although unfortunately, very little work has been done to date to determine Mn toxicity thresholds for zooplankton species. It is possible, however, that Mn may appear to exert greater influence on plankton communities than it actually does, since its concentration is very closely related to lake acidity.

While biological indicators correspond poorly with the observed patterns in rotifer community composition in this study, they should not be discounted. Recent studies have demonstrated the potential for rotifer–crustacean (Gilbert 1985; Gilbert and Stemberger 1985) and rotifer–insect (Moore and Gilbert 1987) interactions. However, additional non-acid lakes need to be analyzed to determine the extent of these interactions.

We conclude that our results, when combined with those of Carter et al. (1986), indicate that rotifer community structure in eastern Canadian lakes subject to acidification becomes increasingly predictable as their assemblages become simpler. These patterns complement those previously established for crustacean zooplankton assemblages in acidic metal-contaminated Ontario lakes (Carter 1971; Sprules 1975). Thus, the response of rotifer communities does not appear to be unique. Circumneutral lakes in our study typically demonstrated greater diversity and heterogeneity than their acidic counterparts and as a result, recurrent patterns in species distributions in non-acid lakes were more difficult to discern and community structure was less clearly defined than in acid lakes.

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Appendix

Comparison of chemical parameters for two study lakes. Samples from 1981, 1982, and 1983 were analyzed by the Ontario Ministry of the Environment, while 1984 samples were analyzed at the University of Toronto using inductive coupled plasma (ICP) emission spectroscopy. All values are based on analysis of single samples (W. Keller, unpubl. data). —, not available.

	Clearwater			Tilton			
Parameter	Aug. 1981	July 1982	July 1984	Aug. 1981	Aug. 1982	Aug. 1983	July 1984
pH	4.52	4.48	4.65	5.00	5.11	5.08	5.23
Mg ($mg \cdot L^{-1}$)	1.5	1.4	1.3	1.2	1.2	1.1	1.1
Na ($mg \cdot L^{-1}$)	2.0	—	2.2	1.4	—	1.4	1.4
K ($mg \cdot L^{-1}$)	0.55	—	0.58	0.40	—	0.42	0.44
Ca ($mg \cdot L^{-1}$)	6.0	6.0	5.8	4.8	4.8	4.7	4.6
SiO_3 ($mg \cdot L^{-1}$)	1.35	—	0.85	0.60	—	0.50	0.26
SO_4 ($mg \cdot L^{-1}$)	20.0	19.4	18.1	17.5	15.5	17.5	16.0
Cu ($\mu g \cdot L^{-1}$)	46	58	39	28	35	21	17
Ni ($\mu g \cdot L^{-1}$)	190	230	180	140	150	120	100
Zn ($\mu g \cdot L^{-1}$)	28	35	33	19	28	18	16
Al ($\mu g \cdot L^{-1}$)	200	250	160	110	120	80	64
Mn ($\mu g \cdot L^{-1}$)	286	279	230	140	137	109	86
Fe ($\mu g \cdot L^{-1}$)	40	30	75	110	30	35	70

Biochemical Genetic Survey and Stock Identification of Chum Salmon (*Oncorhynchus keta*) in British Columbia

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Beacham, T. D., A. P. Gould, R. E. Withler, C. B. Murray, and L. W. Barner. 1987. Biochemical genetic survey and stock identification of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. 44: 1702–1713.

We examined genetic variability using electrophoretic analysis of 83 chum salmon (*Oncorhynchus keta*) stocks in British Columbia and used regional differences in genotypic frequencies of seven polymorphic loci to estimate stock compositions in a number of commercial and experimental test fisheries. Chum salmon from five regions could be discriminated: Queen Charlotte Islands, north and central coast, west coast of Vancouver Island, the Fraser River and its tributaries, and the south coast (rivers draining into Johnstone Strait and the Strait of Georgia). Allelic frequencies from 33 stocks were generally stable over a period of 2 yr or more. South coast chum salmon was the dominant run migrating through upper Johnstone Strait in October 1982–85. The genetic method of stock identification provided managers with the relative proportions of Fraser River and other groups of chum salmon in a number of fisheries and allowed managers to regulate more effectively the exploitation rate of Fraser River chum salmon.

Les auteurs ont étudié par analyse électrophorétique la variabilité génétique de 83 stocks de saumon kéta (*Oncorhynchus keta*) de la Colombie-Britannique. Ils ont ensuite utilisé les différences régionales des fréquences génotypiques de sept loci polymorphes pour calculer la composition des stocks dans un certain nombre de pêches types commerciales et expérimentales. Ils one pu identifier les saumons kétas de cinq régions : îles de la Reine-Charlotte, littoraux nord et centre, côte ouest de l'île de Vancouver, fleuve Fraser et ses tributaires, et littoral sud (les rivières se déversant dans les détroits de Johnstone et de Georgie). Les fréquences alléliques de 33 stocks ont été généralement stables pendant deux ans ou plus. Le saumon kéta du littoral sud constituait la principale remontée dans la partie supérieure du détroit de Johnstone en octobre, de 1982 à 1985. Cette méthode génétique d'identification des stocks a fourni aux gestionnaires les proportions relatives du nombre de saumons kéta provenant du fleuve Fraser ou d'ailleurs présents dans les pêches et leur a permis de réglementer plus efficacement le taux d'exploitation du saumon kéta du fleuve Fraser.

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Chum salmon (*Oncorhynchus keta*) are widely distributed in coastal British Columbia, spawning in over 800 rivers and streams (Aro and Shepard 1967). Chum salmon show a marked diversity in many life history traits (Beacham and Murray 1987) and stock abundance. Spawning time ranges from July in the northern and central coastal regions of British Columbia to as late as January in the southern region (Neave 1966). There have been marked fluctuations in natural chum salmon abundance in British Columbia since 1920 (Hoar 1951; Beacham 1984), and substantial effort in artifical enhancement of chum salmon through hatcheries and spawning channels has occurred in British Columbia since the 1970s.

Chum salmon are exploited in commercial fisheries throughout coastal British Columbia, and effective regulation of the fisheries with respect to conservation of less productive stocks is an area of continuing concern for fisheries managers. The fisheries range in character from more terminal ones on the Queen Charlotte Islands and northern and central coast regions to a major interception fishery in Johnstone Strait in southern British Columbia. Stock composition is of prime concern to fisheries managers in a mixed stock interception fishery in order to ensure that less productive stocks are not overexploited.

Early work on stock identification of chum salmon in areas of commercial fisheries centered on tagging (Pritchard 1929, 1931; Chatwin 1953; Manzer 1954; Anderson and Beacham 1983), but the results of those studies did not provide managers with the information or the flexibility to regulate the fishery during the fishing season. An effective tagging program is also difficult and expensive to conduct, and thus, alternative methods of stock identification of chum salmon were required.

Variation in scale characters has been used for stock identification in chum salmon (Tanaka et al. 1969; Kovtun 1983; Nikolayeva and Semenets 1983), but in British Columbia it does not provide the resolution or the reliability for managers to regulate the fisheries during the fishing season. Genetically determined protein variation has been reported in chum salmon stocks (Okazaki 1981, 1982; Beacham et al. 1985), and genetic differences among stocks have previously been used in estimat-

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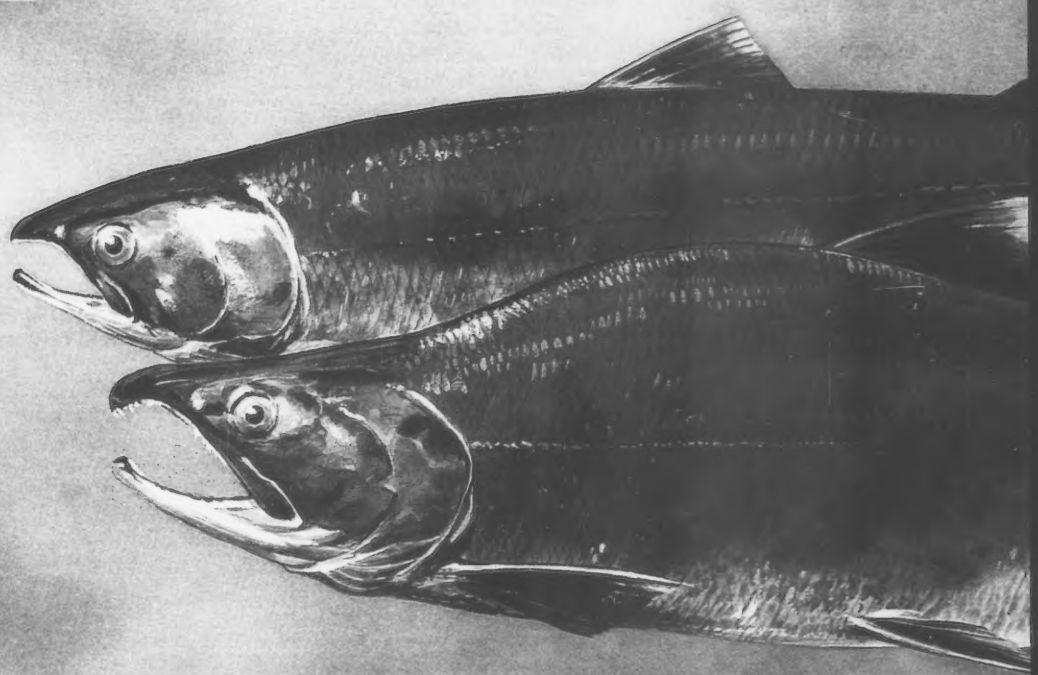
Sockeye Salmon

(Oncorhynchus nerka)

Population Biology and Future Management

Edited by H.D. Smith, L. Margolis, and C.C. Wood



Fisheries and Oceans | Pêches et Océans

Sockeye Salmon *(Oncorhynchus nerka)* Population Biology and Future Management

Edited by H. D. Smith, L. Margolis, and C. C. Wood

A three-day International Symposium on Sockeye Salmon *(Oncorhynchus nerka)* was organized by the Canada Department of Fisheries and Oceans and convened at Nanaimo, British Columbia in November 1985. Advice on subject matter and participation came from an external committee of senior scientists and administrators in contributing agencies in Canada, Japan, the United States, and the Union of Soviet Socialist Republics. The papers included in the proceedings deal with sockeye biology and stock management.

Papers on sockeye biology are divided into those concerned primarily with (a) life history strategies and (b) enhancement and development. Papers dealing with management are divided into (a) the tools of management and (b) management of some principal stocks.

Le ministère des Pêches et des Océans du Canada a organisé un Symposium international sur le saumon nerka *(Oncorhynchus nerka)* qui a eu lieu en novembre 1985 à Nanaimo (Colombie-Britannique). Un comité externe composé de scientifiques principaux et d'administrateurs oeuvrant au sein d'organismes participants du Canada, du Japon, des États-Unis et de l'Union des républiques socialistes soviétiques a fourni des conseils sur les questions étudiées. Les études présentées dans le compte rendu portent sur la biologie et la gestion des stocks de saumon nerka.

Les études sur la biologie du saumon nerka sont divisées en deux grandes catégories, soit a) les variantes du cycle vital et b) la mise en valeur et le développement. Dans le cas des études sur la gestion de stocks, elles sont classées en deux groupes, soit a) les outils de gestion et b) la gestion de certains stocks importants.

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ing stock compositions in salmon fisheries (Grant et al. 1980; Miller et al. 1983). An investigation of the genetic method of stock identification thus seemed appropriate for chum salmon fisheries in British Columbia.

In 1981, we initiated spawning ground collections of chum salmon in southern British Columbia in order to examine genetically based protein variation and its applicability to stock identification. The results of our surveys up to 1983 were subsequently published (Beacham et al. 1985), and in 1984 and 1985 we extended our surveys to include stocks and fisheries not previously examined. In the present study, we outline the results of our surveys of genetically based protein variation in chum salmon and their application to fisheries management.

Methods and Materials

Since 1981, we have surveyed genetically based protein variation by starch gel electrophoresis for approximately 13 000 chum salmon from 83 rivers in British Columbia. A stock was defined as a group of chum salmon originating in a particular river. The surveys included 14 stocks from the Queen Charlotte Islands, 21 stocks from the north and central coasts, 21 stocks from the east coast of Vancouver Island and mainland inlets on the east side of the Strait of Georgia, 15 stocks from the west coast of Vancouver Island, and 12 stocks from the Fraser River and its tributaries (Fig. 1). We have also surveyed in excess of 8000 chum salmon from at least 25 experimental test or commercial fisheries since 1981 (Fig. 1, 2).

Methods of sample collection are outlined in Beacham et al. (1985). Summarized briefly, heart, liver, and muscle samples were collected from adult chum salmon, frozen, and stored at −20°C for later electrophoretic analysis either by ourselves (some test fishery samples) or by a consultant. We verified the scoring of all gels from a complete photographic record. Horizontal starch gel electrophoresis, described by Utter et al. (1974), was used to detect protein variation. The loci and buffer systems used are outlined in Beacham et al. (1985). Tripeptide aminopeptidase (Tapep) was previously labelled Lgg, and mannose-6-phosphate isomerase (Mpi) was previously labelled Pmi. For the duplicated MDH isolocus, we assumed that only one locus of each pair was segregating in the calculation of allelic frequencies. One change from our previous study is the interpretation of Tapep (Lgg). It was previously scored as a two-allele locus examined on a Tris, boric acid, and EDTA buffer described by Markert and Faulhaber (1965). In 1985, Tapep (Lgg) was interpreted in the original manner to be consistent with previous results, and also as a four-allele locus (L. Seeb, University of Idaho, pers. comm.) (although only three were present in the stocks we surveyed) on both the Markert and Faulhaber buffer and an amine citrate described by Clayton and Tretiak (1972).

We used the likelihood-ratio statistic (G-test) (Sokal and Rohlf 1969) to test equality of allelic frequencies among and within geographic regions and between years for samples taken from the same stock. An approximate F-ratio (G-statistic summed over all loci/degrees of freedom) was used to test the relative magnitude of the sources of variation. We calculated genetic distance among stocks using Nei's (1978) statistic and the loci as outlined by Beacham et al. (1985) and constructed a dendogram from the matrix of the distances using the complete linkage method of Sneath and Sokal (1973). The Weaver Creek, Big Qualicum, Cheakamus, and Sliammon stocks were deleted because allelic frequencies for all loci were not available.

We estimated stock compositions in the experimental test or commercial fisheries by the method of Fournier et al. (1984), incorporating the previous baseline sampling reported by Beacham et al. (1985) with the results of the present study, and using the same allocation procedure as previously reported. Thirteen stocks were not included in the baseline samples for the estimation of stock composition. These stocks were not included because they were of insignificant size, of considerably later timing than the fishery sampling, or unlikely to be present in any sample (Taku River). The stocks were as follows: Queen Charlotte Islands — Stanley Creek; north and central coasts — Taku River, Ecstall River, Wannock River, Green River; south coast — Goldstream River, Sliammon Creek, Nimpkish River, Chemainus River, Okeover Creek; Fraser River — Chilqua Slough; and west coast of Vancouver Island — Stevens Creek, Thornton Creek. Seven loci were used to estimate stock compositions: Idh-1, Idh-3, Me, Mpi, Tapep, 6-Pg, and Agp-2. Estimates of the Queen Charlotte Islands, north coast, south coast, Fraser River, west coast of Vancouver Island, and Washington State components were estimated by summing the contributions of the individual group members. For fisheries in southern British Columbia, the Queen Charlotte Islands and north and central coast stocks were removed because we expected no contributions from northern chum salmon stocks in fisheries in southern British Columbia, as the route of migration of returning chum salmon is generally from north to south. Similarly, west coast of Vancouver Island stocks were removed as potential contributors to Johnstone Strait and Strait of Georgia fisheries. We determined standard deviations of the estimates by bootstrap simulations where 50 new mixtures of the same size were constructed by sampling the original mixture with replacement. Stock compositions were then estimated for each of these new mixtures and standard deviations derived from the 50 estimates.

Results and Discussion

Population Structure

Regional differentiation of allelic frequencies for chum salmon in British Columbia was observed. Chum salmon from the Fraser River and north coast had a lower frequency of $Idh\text{-}1^{100}$ than did those from the south coast, the west coast of Vancouver Island, and the Queen Charlotte Islands (Table 1).[2] Chum salmon stocks in regions other than the Queen Charlotte Island were almost monomorphic at 6-Pg. For Me, Queen Charlotte Islands stocks were less variable than those in other regions in British Columbia. Substantial differences in frequencies of $Idh\text{-}3^{100}$ were observed among regions, with Queen Charlotte Islands stocks having the lowest and south coast stocks having the highest frequencies. Regional differentiation was also observed at Agp-2, Mpi, and Tapep.

Variation in allelic frequencies of chum salmon among regions was substantially greater than among stocks within regions ($F_{56,998} = 24.6$, $P < 0.01$) (Table 2), illustrating the possibility of using a genetic method of stock identification in chum salmon fisheries in British Columbia. In order for a genetic method of stock identification to be practical, allelic frequencies should be stable through time to eliminate annual sampling on the spawning grounds. We tested the stability of

[2]Complete set of allelic frequencies by stock is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

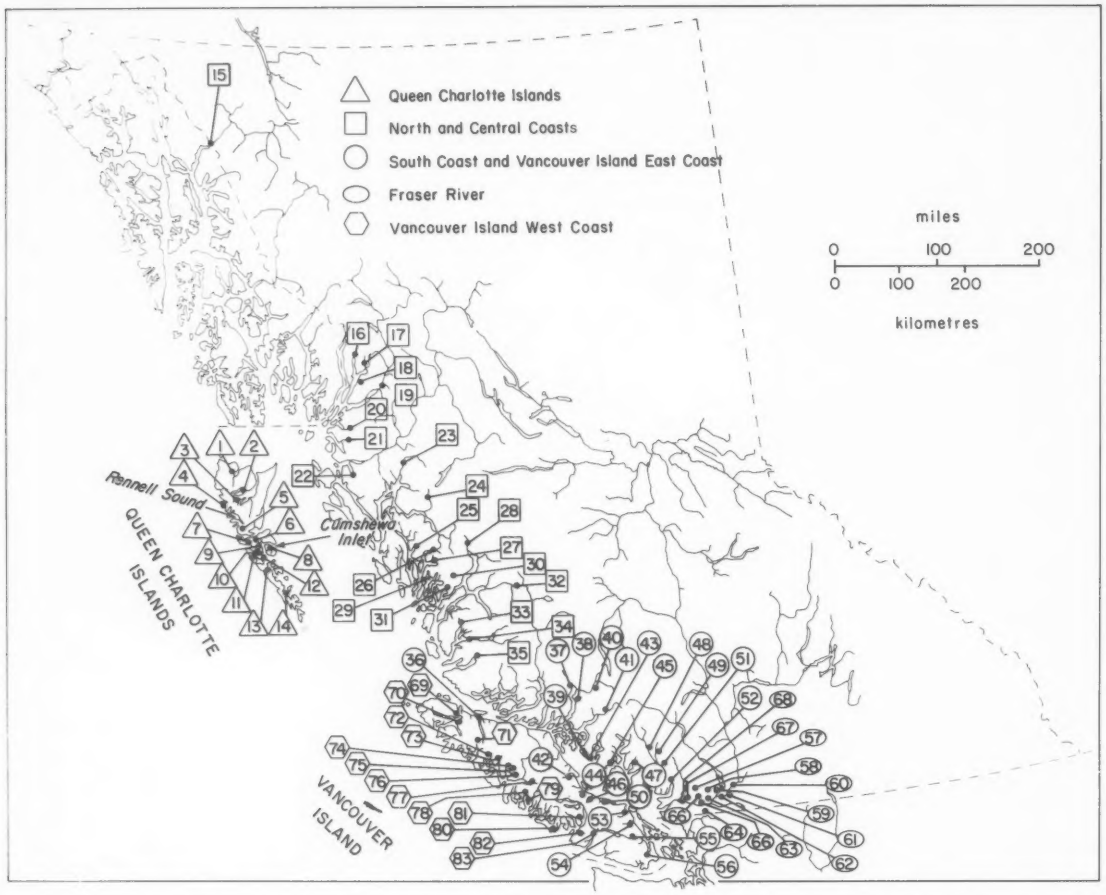

FIG. 1. Locations where chum salmon were sampled during 1981–85. Queen Charlotte Islands: (1) Stanley Cr., (2) Ain R., (3) Awun, (4) Nesto Cr., (5) Lagins Cr., (6) Deena R., (7) Security Cr., (8) Mathers Cr., (9) Pallant Cr., (10) Lagoon Cr., (11) Tasu Cr., (12) Big Goose Cr., (13) Salmon R., (14) Bag Harbour Cr. North coast: (15) Taku R., (16) Kshwan R., (17) Kitsault R., (18) Stagoo R., (19) Nass R., (20) Khutzeymateen R., (21) Toon R., (22) Ecstall R., (23) Kitimat R., (24) Kemano R., (25) Green R., (26) Mussel R., (27) Kainet Cr., (28), Kimsquit R., (29) Cascade R., (30) Neekas Cr., (31) Elcho Cr., (32) Bella Coola R., (33) Clyak R., (34) Wannock R., (35) Nekite R. South coast: (36) Nimpkish R., (37) Homathko R., (38) Orford R., (39) Okeover Cr., (40) Southgate R., (41) Toba R., (42) Puntledge R., (43) Sliammon R., (44) Rosewall Cr., (45) Saltery Bay Cr., (46) Big Qualicum R., (47) Tzoonie R., (48) Squamish R., (49) Cheakamus R., (50) Little Qualicum R., (51) Mamquam R., (52) Indian R., (53) Nanaimo R., (54) Chemainus R., (55) Cowichan R., (56) Goldstream R. Fraser River: (57) Stave R., (58) Chehalis R., (59) Weaver Cr., (60) Fraser R., (61) Wahleach Slough, (62) Harrison R., (63) Squakum Cr., (64) Vedder R., (65) Inch Cr., (66) Chilqua Cr., (67) Alouette R., (68) Blaney Cr. West coast of Vancouver Island: (69) Stevens Cr., (70) Marble R., (71) Tahsish R., (72) Zeballos R., (73) Tahsis R., (74) Sucowa R., (75) Canton R., (76) Conuma R., (77) Burman R., (78) Megin R., (79) Atleo R., (80) Thornton Cr., (81) Nahmint R., (82) Sarita R., (83) Nitinat R.

allelic frequencies by examining two or more loci in 33 stocks for periods ranging from 2 to 4 yr. Of 201 comparisons made for the loci subsequently used in stock identification, 14 (7%) were significant, about the number expected by chance. We conclude that once stocks contributing to a fishery have been surveyed, it is not necessary to conduct annual electrophoretic surveys to obtain reliable estimates of allelic frequencies. Variation in allelic frequencies among stocks within a region was greater than among sampling years within a stock ($F_{998,356} = 2.3$, $P < 0.01$). The greatest variability in allelic frequencies was observed between regions, followed by stocks within regions, with the least variability observed among years within stocks (Table 2).

Heterogeneity in allelic frequencies was greatest among regions, but was also present among stocks within regions. The most heterogeneous grouping of stocks was in the Queen Charlotte Islands (Table 2). This greater heterogeneity may occur because the Queen Charlotte Islands was a refugium during the last ice age, while most other areas of British Columbia were glaciated (Warner et al. 1982). These stocks may thus have had a longer period to accumulate genetic mutations and for genetic drift to occur. The least heterogeneity in allelic frequencies among stocks within a region was observed in the west coast of Vancouver Island and Fraser River groups. These were among the smaller geographic regions examined, and thus it is reasonable to expect that heterogeneity

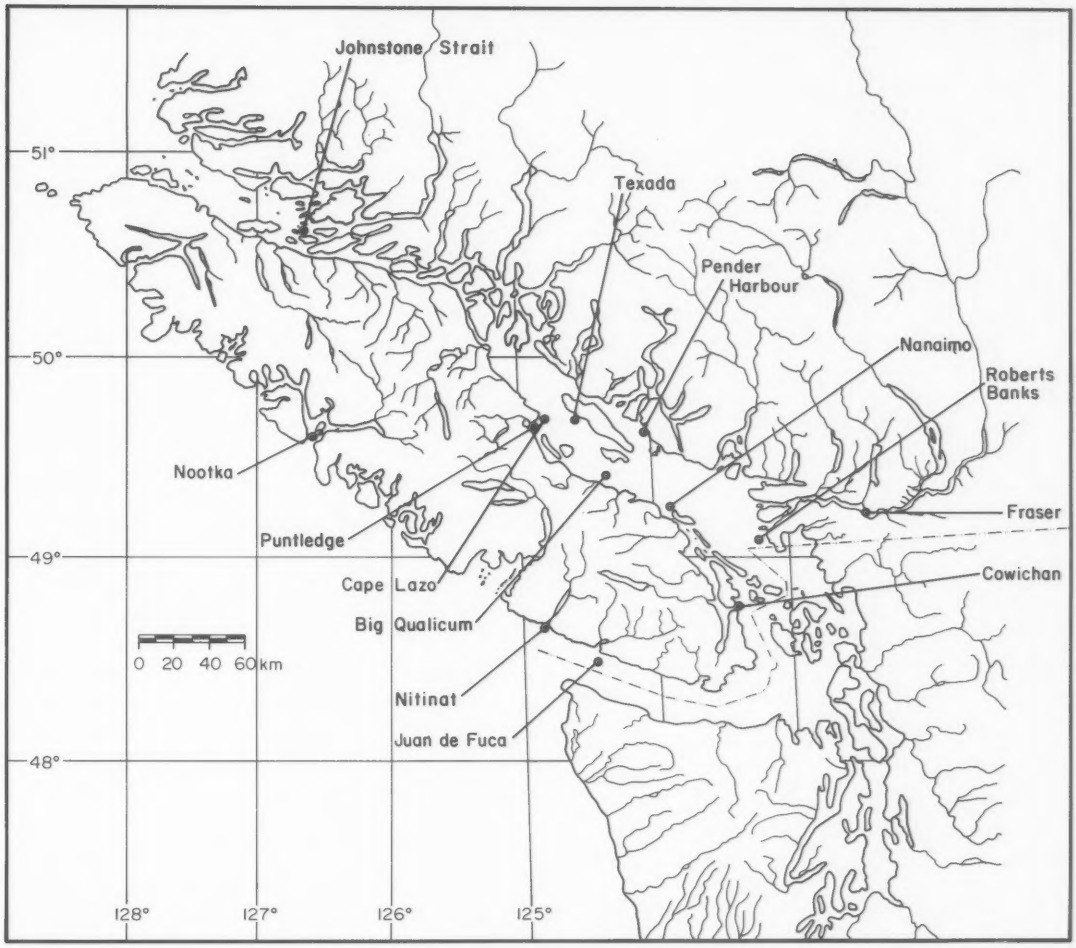

FIG 2. Locations of experimental test and commercial fisheries sampled in southern British Columbia, 1982–85.

in allelic frequencies among stocks would be reduced in these regions.

We examined the standardized genetic variance F_{ST} (Wright 1978) among all populations for the loci subsequently used in stock identification. The F_{ST} values for Idh-1, 6-Pg, Me, Agp-2, Idh-3, Mpi, and Tapep were 0.02, 0.02, 0.01, 0.03, 0.06, 0.01, and 0.01, respectively. This indicated that for these loci between 1 and 6% of the observed genetic variation was due to allelic differentiation among populations, and more than 90% of the variation was common to all populations. An F_{ST} value between 0.05 and 0.15 indicates only moderate differentiation among populations (Hartl 1980).

The analysis of genetic distances (Nei 1978) for all pairwise combinations of the 83 stocks ranged from 0.0000 to 0.0336. A dendrogram based on genetic distance indicated five regional groupings of the chum salmon stocks surveyed: Queen Charlotte Islands, north coast, south coast, west coast of Vancouver Island, and Fraser River (Fig. 3). Chum salmon from the Queen Charlotte Islands had the most distinctive electrophoretic characteristics for any region surveyed in British Columbia. The regional grouping of stocks in the dendrogram is indicative of the regional differentiation of allelic frequencies outlined in Table 1.

Heterozygosity was similar among chum salmon stocks in the five regions. Mean unbiased heterozygosities were 0.196 (SE 0.076), 0.207 (0.070), 0.172 (0.061), 0.192 (0.076), and 0.180 (0.060) for Queen Charlotte Islands, north coast, south coast, west coast of Vancouver Island, and Fraser River chum salmon, respectively, for the loci outlined in Table 1. Chum salmon from the Fraser River and south coast tended to be slightly less heterozygous than those from more northern regions. Our estimates of chum salmon heterozygosity do not include monomorphic loci, and thus our estimates will be larger than those reported for other chum salmon stocks (Okazaki 1982). Kijima and Fujio (1984) found that average heterozygosity is related to effective population size in Japanese chum salmon stocks. More abundant stocks had increased genetic variance. In our survey, north coast and Queen Charlotte Islands stocks had greater heterozygosity than those further south, but stock abundance, particularly for those on the Queen Charlotte Islands, is generally smaller in the northern stocks (Beacham 1984).

TABLE 1. Regional allelic frequencies at polymorphic loci for chum salmon sampled during 1981–85. The most common at a locus designated 100, and

Region	Idh-1		Idh-3						Me		Mpi			
	N	100	N	100	25	40	85	110	N	100	N	100	90	80
Queen Charlotte Islands	1733	0.982	1643	0.286	0.281	0.326	0.105	0.002	1734	0.896	1698	0.931	0.059	0.010
North and central coasts	2737	0.873	2641	0.395	0.170	0.363	0.071	0.001	2735	0.867	2666	0.908	0.088	0.004
South coast and East coast of Vancouver Island	2622	0.935	2711	0.620	0.067	0.269	0.043	0.001	2742	0.786	2660	0.906	0.094	0.000
West coast of Vancouver Island	1891	0.956	1893	0.459	0.166	0.286	0.089	0.000	1892	0.816	1884	0.903	0.097	0.000
Fraser River	1717	0.904	1707	0.587	0.081	0.288	0.044	0.000	1749	0.850	2204	0.877	0.122	0.000

[a]Tapp interpreted as a three-allele locus with mobilities reported on the AC buffer.

Mixed Fishery Analysis

Johnstone Strait

The commercial fishery in Johnstone Strait is the largest mixed stock chum salmon fishery in British Columbia. The entire purse seine fleet in British Columbia may at times be located in Johnstone Strait during fisheries for chum salmon. Johnstone Strait is the major migratory route of chum salmon returning to spawn in rivers on the east coast of Vancouver Island, in the mainland inlets on the east side of the Strait of Georgia, and in the Fraser River and its tributaries (Anderson and Beacham 1983). Chum salmon stocks on the east coast of Vancouver Island and in the Fraser River have been enhanced by either hatcheries or spawning channels at several facilities. Stocks in the mainland inlets have not been enhanced to the same degree.

One of the major concerns of fisheries managers is to provide adequate regulation of the Johnstone Strait fishery to ensure conservation of less productive stocks. In the 1970s and early 1980s, reducing the exploitation rate on Fraser River chum salmon was the goal of fisheries managers. By 1980, fisheries managers knew, from previous tagging studies, that Fraser River and other south coast chum salmon migrated concurrently through Johnstone Strait. No methods were available to identify Fraser River chum salmon, and thus, managers were often thwarted in their efforts to conserve Fraser River chum salmon. Regulation of the Johnstone Strait fishery was based on total abundance of chum salmon entering Johnstone Strait, and lacking the ability to discriminate among stocks, managers could not provide special conservation for Fraser River chum salmon.

Our surveys of biochemical genetic variation of chum salmon began in 1981 with the initial goal of providing managers with the ability to identify Fraser River chum salmon in mixed stock fisheries in Johnstone Strait and the Strait of Georgia. Weekly sampling during September and October of an experimental test fishery in Johnstone Strait began in 1982 and has continued on an annual basis.[3] These samples have been processed within 48 h of collection and estimates of stock composition (Table 3) provided to managers for use in formulation of decisions on the conduct of the fishery.

Chum salmon from the south coast group of stocks comprise the dominant run migrating through Johnstone Strait (Fig. 4). Chum salmon from the Fraser River and south coast were about equal in abundance through the first 3 wk of September during 1982–85, but after that, chum salmon from the south coast were the most abundant group. Chum salmon from Washington State generally comprised less than 5% of the weekly samples in Johnstone Strait (Table 3), although in 1985, Washington State chum salmon were relatively more abundant in Johnstone Strait than in the previous 3 yr. They were most abundant in Johnstone Strait during the last week of September and first 2 wk of October (Fig. 4).

The identification of the relative timing of different runs of chum salmon through Johnstone Strait allows managers more flexibility in the operation of the fishery. If the abundance of chum salmon entering Johnstone Strait is sufficient for opening the fishery for 1 wk only, and if the goal of managers is to minimize interceptions of Fraser River and Washington State chum salmon in a period of significant chum salmon abundance, then an opening about October 15 would seem to be a reasonable option to consider. However, managers also need to consider that the south coast stock group is composed of enhanced and unenhanced stocks, and consideration should be given to avoid overexploitaiton of the unenhanced stocks.

Electrophoretic analysis will not provide reliable information on the relative abundance of a particular stock migrating through Johnstone Strait. Within the Fraser River and south coast stock groups, there is not sufficient detectable electrophoretic variation among stocks that would unequivocally identify a particular stock in the interception fishery. If this information becomes critical for management, either more potentially discriminating alleles will have to be found or techniques for stock identification other than electrophoretic analysis will have to be examined.

Other Fisheries

Biochemical genetic stock identification has been used in the management of actual commercial fisheries or development of

[3]Complete set of weekly allelic frequencies is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

other alleles were assigned numbers according to the mobility relative to that of the 100 allele. *N* is number of fish scored at each locus.

6-Pg		Agp-2		Tapep		Tapep[a]				Mdh-1,2		Mdh-3,4			
N	100	N	100	N	100	N	100	50	75	N	100	N	100	120	65
1731	0.956	1622	0.873	1605	0.763	69	0.674	0.246	0.080	1733	0.999	1736	0.991	0.009	0.000
2725	0.993	2541	0.863	2729	0.812	1081	0.795	0.175	0.030	2740	1.000	2736	0.996	0.002	0.002
2768	0.999	2541	0.956	1698	0.824					2706	0.999	2767	0.998	0.002	0.000
1892	0.997	1817	0.958	1881	0.772	1088	0.648	0.290	0.062	1897	0.999	1894	0.996	0.002	0.002
1750	0.994	2127	0.940	1133	0.826					1772	1.000	1767	0.998	0.002	0.000

potential ones in several areas in southern British Columbia.[4] At the Big Qualicum River on the east coast of Vancouver Island, a spawning channel has been very successful in increasing chum salmon production since the late 1960s. Stocks in the Little Qualicum and Puntledge rivers (Fig. 1) have been recently enhanced with production from a spawning channel and hatchery, respectively. The increased enhanced production required regulation of fisheries to harvest the enhanced stocks without overexploiting less productive stocks. The practice has been to harvest surplus production from enhanced stocks in more terminal fisheries, even though fish quality is lower than in interception fisheries in Johnstone Strait (Hop Wo et al. 1987).

In 1983, Johnstone Strait was closed to a commercial chum salmon fishery, owing to low chum salmon abundance (Fig. 4) and conservation of Fraser River chum salmon. The enhanced stocks could have been exploited in Johnstone Strait, but because they were mixed with wild stocks whose abundance was much reduced, no fishery was conducted. During the 1983 terminal fishery at Qualicum, most of the commercial gear was concentrated along the eastern boundary of the fishing area, as far out into the Strait of Georgia as was legally possible. An unusual number of bright and semibright (salmon just beginning to show the physical changes associated with the onset of sexual maturity) chum salmon was noted in the catch, and a subsequent single sample in the Cape Lazo area indicated that about 40% of the test catch was of Fraser River origin (Table 4). The fishing industry was concerned to learn that while the high-quality chum salmon fishery in Johnstone Strait was closed to help conserve Fraser River chum salmon, Fraser River chum salmon were intercepted in a lower quality chum salmon fishery at Qualicum.

The experience in 1983 led to changes in the 1984 and subsequent Qualicum fisheries. In 1984, fishing areas remained closed when Fraser River chum salmon constituted more than 10% of the samples. Samples for electrophoretic analysis were collected and analyzed from all fishing areas. The management decision opening any area was based on whether Fraser River stocks constituted 10% or greater of the sample. Commercial fishing occurred only near the shore of Vancouver Island (the Qualicum "inside" area), as less than 10% of the fish in these samples was allocated to stocks of Fraser River origin (Table 4). The Qualicum "outside" area, corresponding to the area fished in 1983 along the eastern fishing boundary, remained closed because of the presence of Fraser River chum salmon (Table 4). A similar sampling program was repeated in 1985 with similar results (Table 4). Fraser River chum salmon were in higher proportions in areas further out in the Strait of Georgia, as were chum salmon from Washington State. These results seem intuitively reasonable, and the very low proportions of Fraser River chum salmon in the "inside" samples agree with tagging results reported by Anderson and Beacham (1983). Biochemical genetic stock identification has played a major role in the management of the Qualicum fishery.

As mentioned previously, stocks on the east coast of Vancouver Island are being enhanced, and the increasing production will necessitate the development of new commercial fisheries. As with Qualicum, managers wish to structure the fisheries to minimize interceptions of nontarget stocks. Another potential interception fishery is near the Nanaimo River (Fig. 1). In 1982, chum salmon were very abundant (Fig. 4), and a commercial fishery was conducted off Nanaimo well out into the Strait of Georgia. As off Cape Lazo in 1983, an unusual number of bright and semibright chum salmon was caught off Nanaimo in 1982. A sample from the commercial fishery indicated that about 25% were of Fraser River origin and 30% of Washington State origin (Table 4), potentially accounting for the appearance of bright fish in the catch. Managers, wanting to minimize interception fisheries of this kind, conducted further sampling in 1985. The areas sampled were near Vancouver Island (the "inside" samples) and further out (east) in the Strait of Georgia (the "outside" samples), near where the 1982 fishery occurred. Fraser River and Washington State chum salmon were in higher proportions in the "outside" samples, similar to the experience at Qualicum (Table 4). Managers are thus using electrophoretic analysis to structure new fisheries to minimize interceptions of nontarget stocks.

A potential annual fishery is also possible on the Cowichan and Goldstream River stocks. Samples collected in the Satellite Channel area in 1982 and 1985 indicated that interceptions of

[4]Complete set of allelic frequencies for each fishery is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

TABLE 2. Results of *G*-tests of heterogeneity of allelic frequencies among regions, among stocks within regions, and among QCI = Queen Charlotte Islands.

Source of variation	Idh-1		Idh-3		Me		Mpi		6-Pg	
	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*
Among regions	4	512.4**	16	1702.8**	4	250.9**	8	203.3**	4	317.8**
Within regions	78	174.6**	301	862.6**	78	289.9**	119	377.3**	78	225.0**
Fraser River	11	15.5	33	92.2**	11	36.5**	20	40.5**	11	25.4**
South coast	20	22.2	80	185.1**	20	59.8**	19	98.0	20	21.0
QCI	13	57.8**	52	225.2**	13	100.0**	26	74.5**	13	115.6**
North coast	20	54.7**	80	283.1**	20	75.0**	40	102.6**	20	46.6**
West coast	14	24.4*	56	77.0	14	18.6	14	61.7**	14	16.4
Between years	30	34.5	94	135.5	30	21.8	49	72.5**	30	9.0
Fraser River	5	5.9	15	22.2	5	0.4	9	34.6**	5	0.0
Vedder	1	0.2	3	6.5	1	0.0	1	0.0	1	0.0
Harrison	1	1.4	3	3.1	1	0.0	1	0.3	1	0.0
Squakum	1	0.7	3	1.9	1	0.1	1	6.4**	1	0.0
Inch	1	0.2	3	9.6*	1	0.1	2	1.7	1	0.0
Chehalis	1	3.4	3	1.1	1	0.2	3	1.0	1	0.0
Alouette	0	—	0	—	0	—	1	25.2**	0	—
South coast	5	3.6	15	19.2	5	7.5	8	6.4	5	1.6
Nanaimo	1	0.7	4	5.7	1	1.3	1	0.2	1	1.5
Little Qualicum	1	0.1	3	4.5	1	0.6	1	0.1	1	0.0
Puntledge	1	2.2	4	3.1	1	3.5	1	1.2	1	0.0
Chemainus	1	0.6	1	0.7	1	-1.8	0	—	1	0.1
Toba	1	0.0	3	5.2	1	0.3	2	4.6	1	0.0
Saltery	0	—	0	—	0	—	1	0.0	0	—
Cowichan	0	—	0	—	0	—	1	0.0	0	—
Squamish	0	—	0	—	0	—	1	0.3	0	—
QCI	9	5.7	28	46.1	9	1.3	17	15.8	9	2.4
Pallant	2	4.1	6	6.1	2	0.5	4	3.3	2	1.0
Lagoon	1	0.5	3	7.7	1	0.0	2	3.0	1	1.4
Deena	1	0.0	3	0.4	1	0.0	2	0.3	1	0.0
Ain	1	0.0	3	5.1	1	0.0	1	2.2	1	0.0
Lagins	1	0.2	3	1.5	1	0.4	2	3.1	1	0.0
Salmon	1	0.0	4	5.4	1	0.0	2	1.3	1	0.0
Tasu	1	0.0	3	13.2**	1	0.0	2	1.1	1	0.0
Mathers	1	0.9	3	6.7	1	0.4	2	1.5	1	0.0
North coast	7	13.4	23	35.8	7	11.2	11	15.2	7	4.5
Nekite	1	2.5	3	0.6	1	0.2	1	0.0	1	0.0
Bella Coola	1	0.9	4	1.6	1	4.6*	1	0.0	1	0.0
Kitsault	1	4.2*	3	5.7	1	3.6	2	3.3	1	0.5
Stagoo	1	0.0	3	17.0**	1	2.1	2	6.2*	1	3.5
Kshwan	1	3.2	3	1.4	1	0.0	2	3.8	1	0.5
Kimsquit	1	0.7	3	4.2	1	0.1	1	0.0	1	0.0
Kemano	1	1.9	4	5.3	1	0.6	2	1.9	1	0.0
West coast	4	5.9	13	12.2	4	1.4	4	0.5	4	0.5
Conuma	1	4.0*	3	5.3	1	0.0	1	0.2	1	0.0
Nitinat	1	0.1	4	2.8	1	0.4	1	0.3	1	0.5
Scarita	1	0.0	3	2.6	1	0.1	1	0.0	1	0.0
Atleo	1	1.8	3	1.5	1	0.9	1	0.0	1	0.0
Total	112	721.5	411	2700.9	112	562.6	176	653.1	112	551.8

nontarget stocks should be minimized in the area (Table 4). Sampling near Pender Harbour on the mainland side of the Strait of Georgia indicated substantial mixing of Fraser River and south coast chum salmon (Table 4). If the goal is to minimize interceptions of Fraser River chum salmon, no terminal fishery is possible in the location sampled. Sampling on Roberts Bank near the mouth of the Fraser River indicated that at times there may be substantial mixing of Fraser River and south coast chum salmon (Table 4), as well as a Washington State component.

So far we have discussed only those fisheries occurring in Johnstone Strait or the Strait of Georgia, but the issue of determining whether a fishery is an interception one or not is central to most chum salmon fisheries in British Columbia. In September 1985, unusually large chum salmon catches were recorded by trollers fishing off the west coast of the Queen Charlotte Islands. Sampling in Rennell Sound indicated that over 90% of the fish were of Queen Charlotte Islands origin, with the remainder allocated principally to the west coast of

years within stocks from chum salmon sampled in British Columbia during 1981–85 (*$P < 0.05$, **$P < 0.01$).

Agp-2		Tapep		Mdh-1,2		Mdh-3,4		Total		Standardized measure
df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	
4	487.5**	4	172.1**	4	1.5	8	76.6**	56	3724.9**	66.5
77	243.6**	77	302.4**	78	42.2	112	160.1*	998	2677.7**	2.7
11	22.9*	10	29.8**	11	3.4	11	14.9	129	281.1**	2.2
19	63.2**	20	102.4**	20	14.0	20	16.1	238	581.8**	2.4
13	71.4**	13	76.0	13	7.7	13	33.1**	169	761.3**	4.5
20	50.6**	20	81.7**	20	5.3	40	59.2*	280	758.8**	2.7
14	35.5**	14	12.5	14	11.8	28	36.8	182	294.7**	1.6
37	46.0	20	52.2	30	6.1	36	38.5	356	416.1*	1.2
9	17.7**	1	0.8	5	0.1	5	0.5	59	82.2*	1.4
1	0.1	0	—	1	0.1	1	0.4			
1	0.3	0	—	1	0.0	1	0.0			
1	1.2	0	—	1	0.0	1	0.0			
2	7.9*	0	—	1	0.0	1	0.1			
3	7.9*	1	0.8	1	0.0	1	0.0			
1	0.3	0	—	0	—	0	—			
8	6.1	1	0.6	5	0.1	5	1.6	57	46.7	0.8
1	0.3	0	—	1	0.0	1	1.4			
1	1.5	0	—	1	0.1	1	0.1			
1	0.3	0	—	1	0.0	1	0.1			
0	—	0	—	1	0.0	1	0.0			
2	2.2	1	0.6	1	0.0	1	0.0			
1	0.0	0	—	0	—	0	—			
1	0.2	0	—	0	—	0	—			
1	1.6	0	—	0	—	0	—			
9	13.0	7	38.5	9	5.9	9	23.1	106	151.8**	1.4
2	9.5**	1	2.9	2	5.9	2	23.0**			
1	0.1	1	25.1**	1	0.0	1	0.1			
1	0.0	1	1.7	1	0.0	1	0.0			
1	0.0	1	4.4*	1	0.0	1	0.0			
1	0.0	1	1.1	1	0.0	1	0.0			
1	0.5	1	2.7	1	0.0	1	0.0			
1	2.9	1	0.6	1	0.0	1	0.0			
1	0.0	0	—	1	0.0	1	0.0			
7	2.2	7	10.8	7	0.0	10	8.8	86	101.9	1.2
1	0.1	1	0.1	1	0.0	1	0.5			
1	0.4	1	2.9	1	0.0	2	2.7			
1	1.1	1	0.7	1	0.0	1	0.0			
1	0.0	1	2.9	1	0.0	1	1.4			
1	0.0	1	0.6	1	0.0	2	2.8			
1	0.1		3.3	1	0.0	2	1.4			
1	0.5	1	0.3	1	0.0	1	0.0			
4	7.0	4	1.5	1	0.0	7	4.5	48	33.5	0.7
1	3.7	1	1.2	1	0.0	2	1.4			
1	3.3	1	0.1	1	0.0	2	1.4			
1	0.0	1	0.0	1	0.0	2	1.7			
1	0.0	1	0.2	1	0.0	1	0.0			
118	777.1	101	526.7	112	49.8	156	275.2	1410	6818.7**	4.8

Vancouver Island (Table 4). Peak spawning of west coast of Vancouver Island chum salmon stocks occurs in October (Lightly et al. 1985), and thus the presence of this group off the west coast of the Queen Charlotte Islands seems plausible. Sampling in Cumshewa Inlet on the east coast of the Queen Charlotte Islands also indicated that a very high proportion of Queen Charlotte Islands chum salmon was present (Table 4).

Fisheries sampled off the west coast of Vancouver Island in Nootka Inlet and off Nitinat River had west coast of Vancouver Island chum salmon as the major stock component (Table 4). Estimated stock compositions for the 1984 and 1985 Nitinat fisheries were reasonably consistent at about 75% west coast of Vancouver Island and 20% south coast.

The biochemical genetic stock identification program has also provided information on migratory routes of Fraser River chum salmon. Although both sockeye salmon (*O. nerka*) and pink salmon (*O. gorbuscha*) approach the Fraser River either through Johnstone Strait and then through the Strait of Georgia

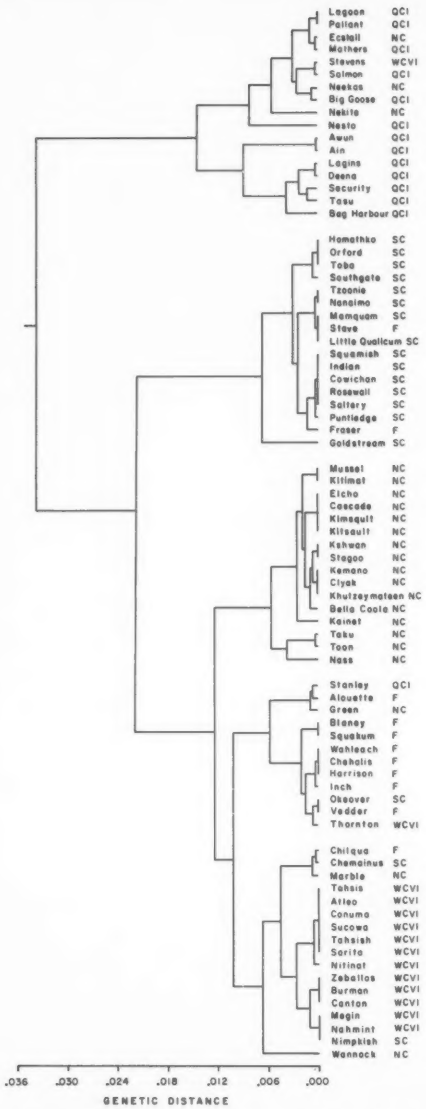

FIG. 3. Dendrogram produced from cluster analysis using Nei's (1978) genetic distance value. QCI = Queen Charlotte Islands. NC = north and central coasts, SC = south coast, F = Fraser River, WCVI = west coast of Vancouver Island.

or along the west coast of Vancouver Island and then through Juan de Fuca Strait (Henry 1961; Verhoeven and Davidoff 1962; Vernon et al. 1964), Fraser River chum salmon were thought to migrate entirely from the north through Johnstone Strait (Palmer 1972; Anderson and Beacham 1983). Sampling in the Canadian portion of Juan de Fuca Strait between October 2 and 16, 1985, indicated that Fraser River chum salmon were present in the southern approach to the Fraser River (Table 4). Like sockeye and pink salmon, chum salmon may have two routes of return to the Fraser River, but the majority of the run uses the northern approach through Johnstone Strait.

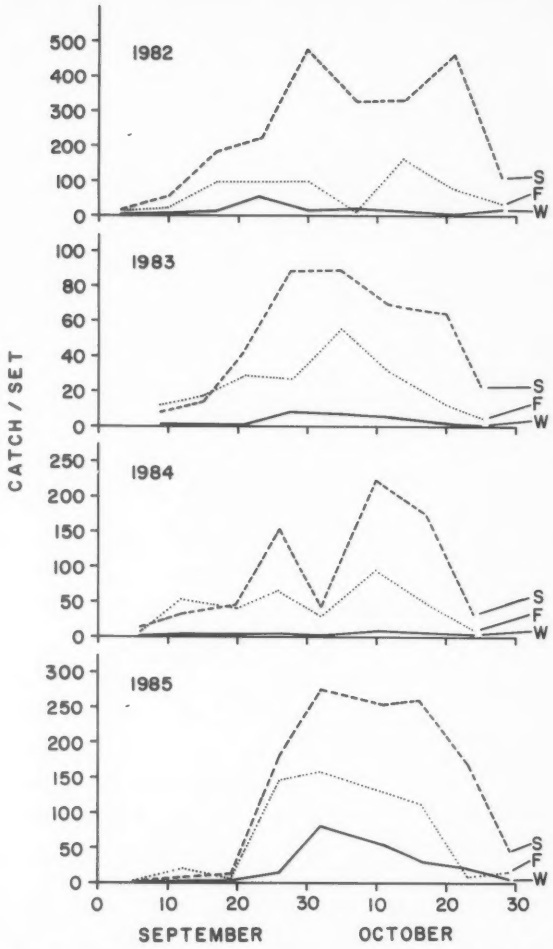

FIG. 4. Mean weekly catch per set from Fraser River, south coast, and Washington State chum salmon in the upper Johnstone Strait purse seine test fishery, 1982–85.

In our survey of biochemical genetic variation of chum salmon in British Columbia, we examined 83 stocks and sampled about 13 000 chum salmon. Sample sizes varied for both the number of fish sampled per stock and also for each locus, but in most cases, at least 100 fish were sampled per stock. We believe that this sampling effort is adequate to provide reasonably accurate estimates of genotypic frequencies for the stocks examined. The regional differences in allelic frequencies appear sufficient to provide discrimination among the regions (Fig. 3). Although chum salmon spawn in 880 rivers in British Columbia (Aro and Shepard 1967) and we have surveyed only 83 rivers, we concentrated on sampling the major spawning stocks in each region. In the Fraser River and south coast regions, stocks that we sampled comprised in excess of 80% of the regional escapement (Beacham et al. 1985), and a similar magnitude of coverage was obtained in the other regions. We thus believe that we have conducted sufficient sampling to provide a reliable estimate of regional stock contribution. We assume that the unsampled stocks within a

TABLE 3. Estimated percentage stock compositions for weekly sampling of the upper Johnstone Strait test fishery. Regions are Fraser River, south coast, and Washington State. Standard deviations are in parentheses. *N* is number of fish sampled in each week.

	N	Fraser	South	Washington
1982 sampling				
September 4	109	50.6 (21.4)	48.1 (21.5)	1.4 (2.8)
September 10	104	32.9 (17.8)	60.3 (16.1)	6.8 (7.1)
September 17	110	34.1 (21.8)	61.6 (22.5)	4.3 (3.5)
September 23	109	24.7 (16.6)	59.9 (15.5)	15.5 (11.0)
October 2	120	16.0 (13.9)	81.7 (13.3)	2.4 (4.8)
October 7	120	2.4 (5.8)	94.0 (6.7)	3.6 (4.2)
October 15	120	32.2 (15.0)	64.3 (16.3)	3.6 (5.8)
October 21	42	14.6 (18.5)	85.1 (18.6)	0.4 (1.0)
October 28	120	18.1 (16.9)	71.7 (16.2)	10.2 (10.1)
1983 sampling				
September 8–9	77	56.3 (19.7)	42.0 (19.8)	1.7 (4.3)
September 14–16	101	53.7 (18.2)	43.0 (16.0)	3.4 (4.8)
September 20–22	100	41.3 (16.2)	58.6 (16.2)	0.1 (0.1)
September 27–30	100	21.5 (16.9)	71.6 (16.8)	7.0 (7.3)
October 3–6	100	37.6 (19.0)	57.6 (16.3)	4.8 (7.1)
October 10–13	100	30.0 (15.8)	65.4 (14.7)	4.7 (4.9)
October 18–21	99	16.2 (11.6)	83.0 (11.6)	0.9 (1.9)
October 24–26	100	18.7 (13.2)	81.1 (13.5)	0.3 (0.7)
1984 sampling				
September 5–7	95	40.0 (21.3)	59.8 (21.0)	0.2 (0.9)
September 11–13	99	60.6 (14.7)	37.7 (14.5)	1.8 (3.1)
September 19–21	98	45.8 (19.8)	50.2 (18.9)	4.0 (5.3)
September 25–28	100	29.9 (17.1)	67.9 (16.6)	2.3 (4.7)
October 1–4	129	37.2 (15.6)	59.4 (15.0)	3.5 (5.6)
October 9–12	88	29.6 (16.9)	67.5 (15.9)	3.0 (4.3)
October 16–19	151	21.2 (11.5)	76.0 (11.2)	2.9 (3.8)
October 22–25	150	19.6 (14.9)	79.3 (15.1)	1.2 (3.3)
1985 sampling				
September 4–6	107	73.5 (15.2)	21.5 (13.5)	5.1 (5.4)
September 11–13	146	72.2 (14.9)	23.8 (15.3)	4.0 (5.8)
September 18–20	153	40.2 (11.8)	53.0 (12.2)	6.8 (5.7)
September 24–27	153	43.1 (14.9)	53.1 (15.0)	3.9 (4.3)
October 1–4	152	30.7 (15.5)	53.4 (13.8)	16.0 (7.5)
October 10–13	148	29.3 (13.9)	58.3 (15.1)	12.5 (7.5)
October 15–18	151	28.5 (13.7)	64.1 (14.6)	7.5 (7.6)
October 22–25	149	4.0 (8.4)	86.6 (9.4)	9.4 (7.5)
October 28–30	152	23.8 (13.5)	68.6 (13.7)	7.6 (5.8)

region have genotypic frequencies more similar to the stocks that we sampled in the region than to stocks in another region.

The annual stability of allelic frequencies of chum salmon that we have demonstrated in our study allows reliable estimates of stock composition to be made during the fishing season before the fish have reached the spawning grounds. Allelic frequencies from other salmonids also appear stable (Grant et al. 1980; Utter et al. 1980), and thus, samples from several years may be pooled. The stability of allelic frequencies makes annual sampling on the spawning grounds unnecessary, unlike scale analysis, where variation in the characters used in stock separation makes annual sampling mandatory (e.g. McBride and Marshall 1983) and restricts the utility of scale analysis for aiding management decisions during the fishing season.

The precision of the estimated stock compositions is dependent on the regional distinctiveness of the allelic frequencies and the number of fish sampled in the mixtures. Queen Charlotte Islands chum salmon stocks are distinctive genetically, and standard deviations of the Queen Charlotte Islands component in the 300-fish mixtures from Rennell Sound and Cumshewa Inlet are less than those of the south coast or Fraser River component from 300-fish mixtures in southern British Columbia (Table 4). Precision of the estimated stock compositions increases as the number of fish sampled in the mixture increases (Beacham et al. 1985), with the most precise estimates recorded in our study derived from the 650-fish mixture of the 1984 Qualicum "inside" sampling. The number of fish sampled in a mixture will depend on the required precision of the estimates and the cost of collecting and processing the samples.

We believe that the biochemical genetic method of stock identification for chum salmon has had considerable influence in the management of commercial fisheries, particularly since 1983 in southern British Columbia. The genetic method of stock identification for chum salmon has been used in the implementation of the terms of the Pacific Salmon Treaty between Canada and the United States and in domestic management concerns such as fishing boundaries and catch quotas by gear type. As well as providing managers with information on these technical issues, we suggest that the application of genetic stock identification to fisheries can result in significant improvement

TABLE 4. Estimated percentage stock compositions for a number of experimental test or commercial fisheries in British Columbia, 1982–85. Regions are Fraser River, south coast, west coast of Vancouver Island (WCVI), Washington State, Queen Charlotte Islands (QCI) and north coast. Standard deviations are in parentheses. *N* is number of fish sampled in each week.

	Year	*N*	Fraser	South	WCVI	Washington	QCI	North
Nanaimo	1982	95	24.7 (18.8)	43.2 (15.1)		32.2 (14.0)		
Cowichan	1982	189	10.0 (8.3)	86.4 (9.0)		3.7 (4.7)		
Puntledge	1982	251	6.7 (5.9)	86.0 (8.4)		7.4 (7.1)		
Fraser	1982	488	80.4 (9.2)	17.8 (7.9)		2.8 (3.3)		
Texada	1982	111	4.3 (5.1)	94.6 (6.2)		1.1 (2.1)		
Cape Lazo	1983	100	37.0 (12.3)	60.2 (12.7)		2.8 (5.1)		
Roberts Bank	1983	188	58.3 (11.9)	35.1 (11.3)		6.7 (4.6)		
Roberts Bank	1984	260	41.2 (14.1)	46.2 (11.6)		12.7 (7.1)		
Big Qualicum								
Inside	1984	649	4.3 (3.5)	93.7 (3.0)		2.0 (1.9)		
Outside	1984	332	24.3 (8.1)	73.2 (8.3)		2.6 (3.2)		
Nitinat	1984	249	3.1 (4.1)	17.1 (7.4)	79.8 (7.3)*	0.0 (0.0)		
Roberts Bank	1985	113	85.8 (10.0)	3.6 (6.1)		10.7 (8.9)		
Big Qualicum								
Inside	1985	588	10.0 (6.7)	86.2 (7.5)		3.7 (3.1)		
Outside	1985	168	8.3 (10.0)	73.0 (11.0)		18.7 (7.5)		
Nitinat	1985	429	5.0 (3.3)	19.3 (7.1)	71.5 (8.3)	4.3 (3.7)		
Pender Hbr.	1985	250	43.1 (18.1)	51.6 (17.6)		5.4 (4.8)		
Rennell Sd.	1985	300	0.2 (0.2)	0.8 (0.3)	6.6 (6.1)	0.0 (0.0)	90.9 (6.5)	1.5 (1.9)
Cumshewa In.	1985	300	0.7 (0.5)	0.3 (0.2)	1.4 (2.8)	0.0 (0.0)	93.8 (4.5)	3.8 (3.2)
Nanaimo								
Inside	1985	428	10.0 (9.4)	83.8 (10.1)		6.2 (4.9)		
Outside	1985	331	28.3 (12.2)	62.9 (10.6)		8.8 (5.6)		
Cowichan	1985	149	12.7 (10.1)	78.2 (10.4)		9.2 (8.7)		
Juan de Fuca	1985	395	30.2 (9.6)	10.0 (7.8)	40.6 (7.0)	19.3 (5.5)		
Nootka	1985	139	2.8 (4.0)	2.0 (3.8)	87.2 (7.8)	8.0 (6.1)		

in the status of the chum salmon resource. Managers were particularly concerned over the status of Fraser River chum salmon. The target escapement of 700 000 fish had not been obtained since 1968 (Beacham and Starr 1982), even though there had been substantial returns of chum salmon to southern British Columbia in 1972, 1973, 1978, and 1982. In 1985, escapement of Fraser River chum salmon was in excess of 900 000 fish, and in 1986 it was in excess of 800 000 fish. The increase in abundance of Fraser River chum salmon may be due to a number of factors, including a refinement in the management of the Johnstone Strait fishery, but we suggest that the ability to identify Fraser River chum salmon by the genetic method of stock identification has been a key component in the management of the run. Managers now have the necessary information on stock composition in a timely manner and can provide more effective management of Fraser River chum salmon.

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Impact of Fenvalerate on Enclosed Freshwater Planktonic Communities and on in situ Rates of Filtration of Zooplankton

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The treatment of large-volume (~ 125 m^3) in situ lake enclosures with fenvalerate at realistic field levels of agricultural contamination by drift or overspray (0.4–4.0 g fenvalerate·ha^{-1}) resulted in the disruption of the structure and function of the planktonic communities. The toxic effects ranged from short-term changes in the feeding behaviour of several species of zooplankton (*Daphnia* spp. and *Ceriodaphnia lacustris*) at 0.05μg fenvalerate·L^{-1} to a drastic reduction in the densities of most of the major groups of zooplankton at 0.1 μg fenvalerate·L^{-1} for periods of up to 3 wk following treatment. In addition, indirect effects of toxicity were observed, e.g. populations of rotifers and phytoplankton increased in enclosures after the removal of the large-bodied cladocerans. This is thought to be the result of a reduction in competition and grazing, respectively. The emulsifying agents used in the emulsifiable concentrate formulation of fenvalerate were not found to be toxic to zooplankton at concentrations expected after agricultural use. The half-life of fenvalerate in an enclosure treated with a nominal concentration of 0.1 μg·L^{-1} was estimated to be 4.1 d by first-order reaction kinetics.

Le traitement in situ de grands enclos lacustres d'environ 125 m^3 avec du fenvalerate à des teneurs correspondant à une contamination agricole par dérives ou surpulvérisations (0,4–4,0 g ·ha^{-1} de fenvalerate) a entraîné une perturbation de la structure et de la fonction des communautés planctoniques. Les incidences toxiques vont de variations à court terme du comportement alimentaire de diverses espèces de zooplancton (*Daphnia* sp. et *Ceriodaphnia lacustris*) à 0,05 μg·L^{-1} de fenvalerate, à une chute marquée des densités de la plupart des principaux groupes zooplanctoniques à 0,1 μg·L^{-1} de fenvealerate, ceci pendant des périodes allant jusqu'à 3 sem après la pulvérisation. De plus, on a observé des incidences indirectes de la toxicité, notamment une augmentation des effectifs des rotifères et du phytoplancton dans les enclos après la disparition des gros cladocères. Ce phénomène semble être le résultat d'une diminution de la compétition et du broutage, respectivement. Les agents émulsifiants utilisés dans la préparation concentré émulsifiable de fenvalerate ne se sont pas révélés toxiques pour le zooplancton aux concentrations devant résulter d'une utilisation agricole. La demi-vie du fenvalerate dans un enclos traité avec une concentration nominale de 0,1 μg·L^{-1} se situe à 4,1 j (cinétique d'une réaction d'ordre premier).

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As little as 1% of all pesticides produced and used annually in North America to control plant pathogens, insect pests, and weeds are estimated to contact their target organisms (Pimentel and Edwards 1982). The remainder enters the surrounding environment as chemical contaminants, and aquatic ecosystems may become the final sink for some of these pesticides (Willis and McDowell 1982).

In situ enclosures or limnocorrals have been used to assess the effects of pesticides in aquatic ecosystems (Kaushik et al. 1986). The treatment of enclosures with pesticides allows observations of the direct and indirect effects of these chemicals on populations of aquatic organisms by monitoring changes in density, diversity, productivity, and other parameters (Kaushik et al. 1985; Herman et al. 1986). The dissipation of the pesticide in the water over time can also be determined (Solomon et al. 1985, 1986).

Recently, several researchers have suggested that changes in the physiology and/or behaviour of aquatic organisms (e.g. respiration, feeding, swimming performance, etc.) could be used as rapid and sensitive indicators of toxic stress (Sprague 1976; Reeve et al. 1977). Such changes may be the initial responses of an organism to environmental perturbation (Slobodkin 1968) and might help to explain other observations such as reduced survival, growth, or reproduction (Flickinger et al.

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1982). Rates of filtration of particles by zooplankton have been observed to decrease following exposure to various chemicals under laboratory conditions (Geiger and Buikema 1981; Kersting and Van der Honing 1981; Day and Kaushik, 1987). The treatment of enclosures with contaminants not only provides an ideal opportunity to observe changes in community structure but also the effects of a toxicant on in situ rates of filtration of zooplankton which have been rarely observed under natural conditions. Cooley (1977) determined that the filtering activity of *Daphnia retrocurva* found near a canal discharging pulp mill effluent into Nipigon Bay was lower than rates of filtration of the same species found near the middle of Nipigon Bay.

This paper describes the results of studies on the impact of the synthetic pyrethroid, fenvalerate ([RS]-α-cyano-3-phenoxybenzyl[RS]-2-[4-chlorophenyl]-3-methyl-butyrate), and its emulsifying agents on the densities and natural rates of filtration of freshwater planktonic communities contained in enclosures. Fenvalerate is toxic under laboratory conditions to many aquatic invertebrates, especially crustaceans, at very low concentrations (ppt) (Anderson 1982; McKee and Knowles 1986), and the contamination of the aquatic environment with fenvalerate through direct overspray, drift during application, or surface runoff during agricultural use is of obvious concern (Khan 1983). The use of in situ rates of filtration of zooplankton to monitor low levels of contamination with fenvalerate is a new technique which may help to standardize bioassay techniques in the field.

Materials and Methods

The field study was carried out in Lake St. George (43°57′N, 79°26′W), a 10-ha meso-eutrophic kettle lake located near King City, Ontario (pH 7.8–8.6; total hardness (as $CaCo_3$) 46–82 $mg \cdot L^{-1}$; total phosphorus 9.7–51.8 $\mu g \cdot L^{-1}$). The enclosures used in this study were part of a research project conducted by the University of Guelph over a 6-yr period to determine methodology for studying the in situ effects of pesticides on aquatic ecosystems. Details regarding the design, size, construction, and installation of the enclosures in Lake St. George have been described elsewhere (Kaushik et al. 1986).

In 1983, a preliminary investigation was conducted with one enclosure receiving a nominal concentration of 0.1 μg fenvalerate$\cdot L^{-1}$ (emulsifiable concentrate (EC) 300 $g \cdot L^{-1}$) on 14 July with the other enclosure remaining as a control. To simulate direct overspray and/or contamination by spray drift, the pesticide was applied to the water surface using a backpack spray unit according to Solomon et al. (1985). The application was equivalent to a field treatment of approximately 4 g fenvalerate$\cdot ha^{-1}$. The recommended field application rates for agricultural crops range from 55 to 220 g fenvalerate$\cdot ha^{-1}$ (Chapman et al. 1983; Bennett et al. 1983).

Samples for pesticide residue analyses were collected 2 h following treatment and at 1, 2, 4, 7, and 14 d thereafter. Up to day 4, samples were collected from 10 cm below the surface and from 1-, 2-, and 3-m depths in clean, amber-coloured glass solvent bottles (4 L) held in a weighted wire basket. On days 7 and 14, water samples were taken using an integrated water sampler (Solomon et al. 1982). Water (1000–1500 mL) containing the pesticide was extracted with hexane (3 × 100 mL), dried over Na_2SO_4, and concentrated to 1 mL. Clean-up and analysis of samples were according to the methods of Braun and Stanek (1982), and analysis was performed at the Provincial Pesticide Residue Testing Laboratory, University of Guelph. Efficiency of extraction of water samples spiked with technical fenvalerate was >95%. Analytical limits of detection were $<0.005 \mu g \cdot mL^{-1}$.

In 1984, two experiments were conducted as follows. In the first experiment, on June 20, fenvalerate was applied as surface application to three enclosures to obtain a nominal concentration of 0.05 $\mu g \cdot L^{-1}$; an EC blank (the EC formulation without fenvalerate) was applied at a concentration equivalent to 0.05 μg fenvalerate$\cdot L^{-1}$ to one enclosure, and three additional enclosures remain untreated as controls. In a second experiment, on 18 July, three enclosures were treated with a nominal concentration of 0.01 μg fenvalerate$\cdot L^{-1}$, while three separate enclosures remained untreated as controls. The application rates were equivalent to approximately 2 g fenvalerate$\cdot ha^{-1}$ and 0.4 g fenvalerate$\cdot ha^{-1}$, respectively. As application rates were close to the analytical limits of detection, no pesticide residue samples were taken in 1984.

Physical and chemical parameters (Secchi disc, temperature, pH, O_2, POC, DIC, DOC, N, P) were monitored in the water column of each enclosure on a weekly or biweekly basis throughout each experiment. To estimate the density of zooplankton in each enclosure during 1983 and 1984, samples were collected from the water column with a vertically integrating tube sampler (depth 3.5 m) (Solomon et al. 1982) and counted in the laboratory using the methods described in Stephenson et al. (1984, 1986).

Five samples for phytoplankton were collected from each enclosure in 1983 using a 25 mm (O.D.) integrated water sampler (Solomon et al. 1982) to a depth of 3.5 m and pooled. A 115-mL subsample was preserved in Lugol's solution and enumerated in the laboratory, as described in Stephenson et al. (1984).

Individual and Community Rates of Filtration

Daphnia galeata mendotae and *D. retrocurva* were the most abundant daphnids present in the enclosures during the experiments (63–97 and 2–33%, respectively) and for convenience were pooled in this study. Only one species of calanoid, *Diaptomus oregonensis*, was present in Lake St. George. Individual rates of filtration (FR) of *Daphnia* spp., *Ceriodaphnia lacustris*, and *D. oregonensis* were determined using a lO-L grazing chamber (Haney 1971).

In 1983, FRs for all three taxa were determined at a depth of 2.0 m and at −15 d and −6 h before pesticide application and at +6 h and +1, +4, +8, +21, and +58 d after treatment in control and treated enclosures. In 1984, FRs for these same species were determined at depths of 1.5 and 3.0 m and at −15, −8, −1, +0.5, +1, +4, +6, +13, and +21 d for enclosures treated with 0.05 μg fenvalerate$\cdot L^{-1}$ and depths of 3.0 m and at −7, −1, +0.5, +1, +3, +6, and +13 d for enclosures treated with 0.01 μg fenvalerate$\cdot L^{-1}$. Community rates of filtration (CFR) of zooplankton were divided into two size classes (30–80 and >80 μm) and were determined for a number of weeks both pre- and post-treatment during 1984. In all experiments, determinations of filtering rates in each treated enclosure were alternated with determinations of filtering rates in control enclosures.

The Haney chamber was loaded with 2 or 4 mL of radiolabelled green alga, *Chlamydamonas reinhardii* (Day and Kaushik 1987), for either individual or community rates of filtration, respectively. Final concentrations of labelled algae in the grazing chamber ranged from 923 to 1250 cells$\cdot mL^{-1}$ and 475

to 1738 dpm·mL^{-1}. The chamber with algae was lowered to the desired depth and closed. Animals were allowed to feed for a period of approximately 5–7 min. After the feeding period was complete, the chamber was lifted from the water, the entire contents of the chamber were released into a large pail, and the contents of the pail were poured through two stacked sieves of mesh size 80 and 30 μm, respectively. Timing of the feeding period was measured with a stopwatch and began as the chamber doors closed and terminated as the pail was completely emptied into the sieves. A 100-mL aliquot of the water in each chamber was collected for subsequent determination of the radioactivity in the feeding suspension.

For the determination of individual grazing rates, a modification of the method by Chow-Frazer and Knoechel (1985) was utilized. The animals retained by the 80-μm-mesh sieve were backwashed into a large disposable petri dish containing 100 mL of near-boiling water and then collected on an 80-μm-mesh sieve glued to a plastic petri dish with the bottom cut out. The animals were rinsed with 100 mL of filtered lake water and stored frozen on dry ice until analysis. Frozen zooplankton contained on sieves from each grazing experiment were lyophilized in a Virtis freeze-dryer overnight. In the laboratory, an experiment was performed to test the effects of freezing and freeze-drying on the determination of filtering-activity of *D. galeata mendotae*. No significant differences in the filtering rate of this species were noted when fresh animals were compared with similarly treated animals which had undergone freezing and freeze-drying (unpublished data).

Freeze-dried animals stored on sieves were identified at low magnification, measured with an ocular micrometer, and sorted into size classes. *Daphnia* spp. were measured from the middle of the eye to base of the tail spine; size classes for this taxon were 0.50–0.59, 0.60–0.69, 0.70–0.79, 0.80–0.89, 0.90–0.99, 1.00–1.09, and ≥1.10 mm. Length of *C. lacustris* was from the top of the carapace to the base of the tail spine, and size classes were 0.30–0.39, 0.40–0.49, and 0.50–0.59 mm. Only adult female *D. oregonensis* were examined, and length was measured from the front end of the cephalothorax to the posterior margin of the caudal rami.

One to 20 similarly sized animals were gently picked with fine forceps by grasping the antennae or tail spine and placed on a damp 2.1-cm GF/A filter; the filter was placed in a scintillation vial and 2 mL of tissue solubilizer NSC (Amersham Searle Corp.) added. Each vial was heated overnight at 48°C in an incubator to digest animal tissues. After digestion, each vial was returned to room temperature and 0.74 mL of glacial acetic acid added to reduce colour quenching. Fifteen millilitres of the scintillation fluor OCS (Amersham Searle Corp.) was added to each vial which was then vigorously shaken 20 times. After 24 h of dark adaptation, the radioactivity in the animals was determined for a 10-min period in a Packard Tri-Carb scintillation counter after corrections for background and quenching.

To ensure that all the radioactivity in the zooplankton came from ingested material rather than adherence of ^{14}C to the body surface, whenever possible, one to five adult *Diacylops bicuspidatus thomasi* or *Mesocyslops edax* were picked and treated in the manner described above. The radioactivity in adult cyclopoids was close to background levels in all samples, indicating that attachment of ^{14}C-labelled particles to the body of the zooplankton was not an important source of error.

FRs (millilitres per individual per day) of zooplankton were calculated as follows:

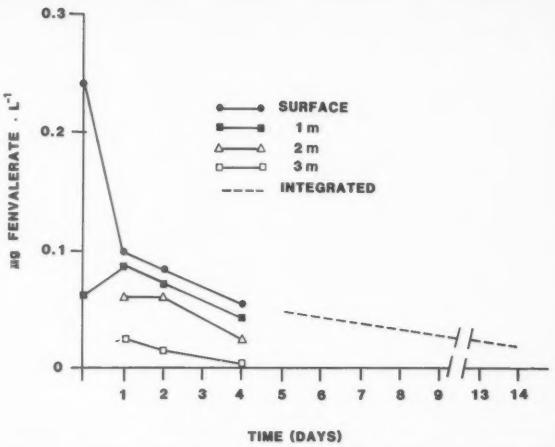

FIG. 1. Concentrations of fenvalerate at different depths in the water column in an enclosure treated with a nominal concentration of 0.1 μg·L^{-1}.

$$FR = \frac{\text{dpm·individual}^{-1}}{\text{dpm·mL water}^{-1}} \times \frac{60 \text{ min} \times 24 \text{ h}}{\text{feeding time (min)}}$$

For the determination of CFR, the contents of the 80- and 30-μm-mesh sieves were backwashed with filtered lake water into large, disposable petri dishes to which 100 mL of near-boiling water was added. The contents of the petri dishes were then sieved again through the 80- and 30-μm-mesh sieves, rinsed with 100 mL of filtered lake water, and preserved with 4% sucrose–formalin. In the laboratory, formalin-preserved zooplankton from each grazing experiment were filtered onto 2.4-cm GF/C filters (Whatman). The filter paper containing zooplankton was placed in a scintillation vial and treated as described above.

Persson (1982) and Holtby and Knoechel (1981) reported a time-dependent loss of radiolabelled material from crustaceans of up to 73% after 3 d of storage in formalin. To account for any such losses in our grazing samples, a 1-mL subsample of the filtrate was placed in a scintillation vial, 12 mL of Aquasol II added, and the radioactivity determined as described above.

CFRs, (millilitres per litre per day) were calculated according to the formula of Lampert and Taylor (1985) as follows:

$$CFR = \frac{\text{dpm in animals}}{\text{dpm·mL chamber water}^{-1}} \times \frac{60 \text{ min} \times 24 \text{ h}}{\text{time spent grazing} \times \text{vol. of chamber (L)}}$$

Evaluation of Impact and Statistical Analysis of Data

For the determination of density, the pelagic zooplankton were divided into five groups: (1) Cladocera, (2) Calanoida (adult *D. oregonensis* plus copepodite stages I–V), (3) Cyclopoida (adults plus copepodite stages I–V), (4) nauplii (both Calanoida and Cyclopoda), and (5) Rotifera. The densities of these groups in the fenvalerate-treated enclosure(s) were compared with those of the control(s) by simply graphing density or mean densities of replicate treatments over time. For statistical analysis of replicated enclosures, a standard *t*-test was performed on the means of the data for control and treated

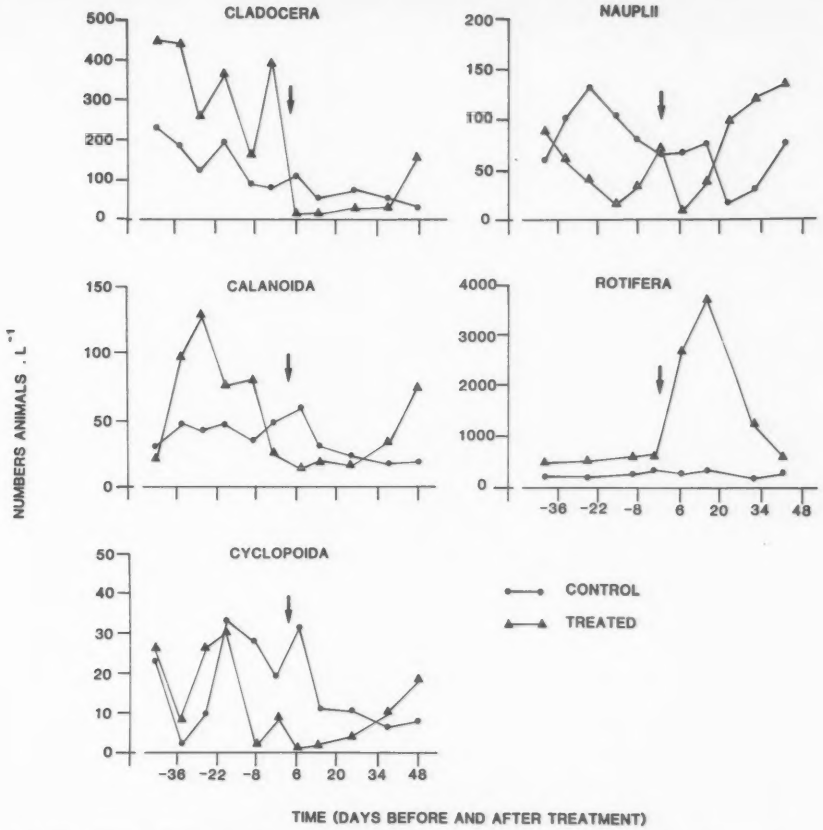

Fig. 2. Changes in the densities of the major groups of zooplankton in a control enclosure and an enclosure treated with 0.1 μg fenvalerate·L^{-1} in 1983. Arrows indicate time of treatment.

enclosures (Steel and Torrie 1980). Prior to statistical analysis, Bartlett's test for homogeneity of variance was performed and, where necessary, data were transformed by log $(x + 1)$. All levels of significance are $P \leq 0.05$ unless otherwise stated.

The impact of fenvalerate on the FRs of *Daphnia* spp., *C. lacustris*, and *D. oregonensis* was determined by comparison of these rates for organisms in control enclosures with FRs of similar-sized organisms in treated enclosures on the same date. In 1983, not enough animals were present to determine statistically acceptable linear regressions of filtering rate versus body length. Therefore, the results of each feeding experiment were expressed as a mean filtering rate for animals of a standard size. The sizes were 0.80–0.90 mm for *Daphnia* spp., 0.50–0.60 mm for *C. lacustris*, and 1.10–10 mm for *D. oregonensis*. Statistical comparison of filtering rates was achieved by the use of *t*-tests as described above.

In 1984, when sufficient animals were available from a particular treatment, the relationship between filtering rate and size was fitted to the linear regression $\log Y = a + b \log X$ (Burns and Rigler 1967) where Y is filtering rate (millilitres per animal per day), X is length (millimetres), and a and b are the intercept and slope, respectively, of the regression line. The evaluation of the impact of fenvalerate on filtration rates of individual species was determined by comparison of the slopes and intercepts of regression lines using the *t*-test. An F-test was used to determine the significance of the linear correlation (APL Statspac, University of Guelph).

Results

Pesticide Residue in Water

Residues of the pesticide in the enclosure treated with a nominal concentration of 0.1 μg·L^{-1} 1983 were highest in the surface to 1 m layer (0.240 μg·L^{-1} maximum) but rapidly decreased over time (Fig. 1). Concentrations at or below 2 m were not detectable 2 h following treatment but were measureable after 24 h, indicating that the pesticide had moved through the water column. At 4 d following treatment (the last sampling date for separate depth samples), the pesticide was not detectable at 3 m but appreciable levels were still present at shallower depths. By 14 d following treatment, levels of fenvalerate in an integrated sample were approximately 0.010 μg·L^{-1}.

Data for the dissipation of fenvalerate over time fitted the first-order kinetic model $Y = 4.37 + (-0.17X)$ ($r^2 = 0.76$; $P = 0.05$). The time to 50 and 90% dissipation was estimated to be 4.1 and 13.5 d, respectively.

Physical and Chemical Water Parameters

There were few differences in the physical and chemical

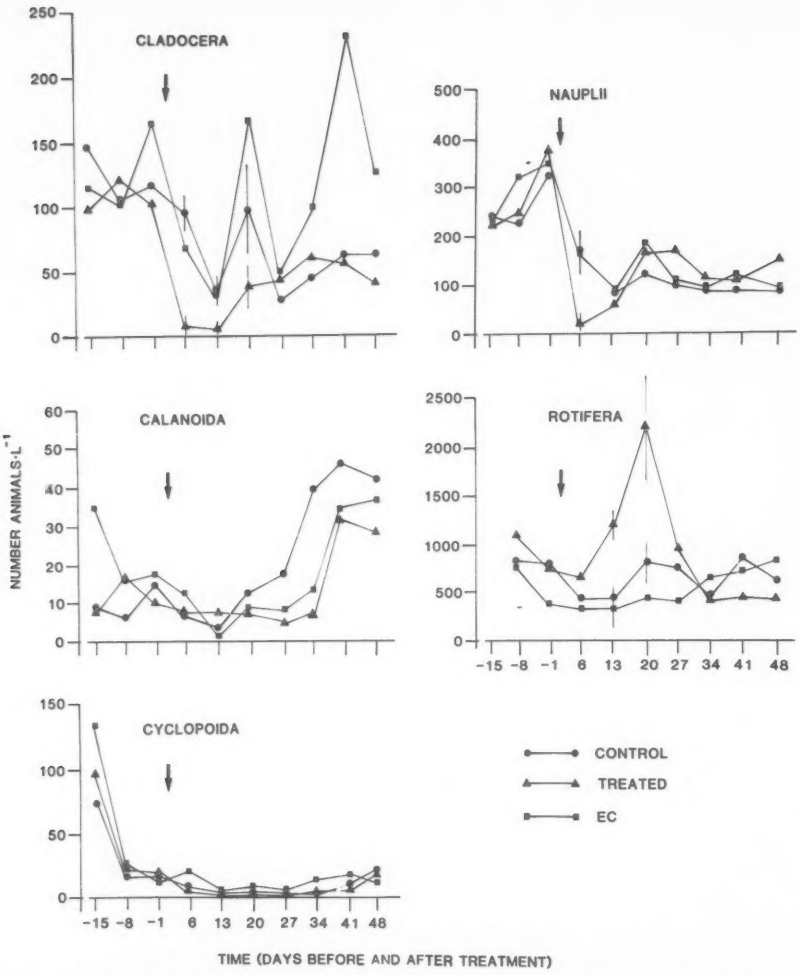

FIG. 3. Changes in mean densities of the major groups of zooplankton in control enclosures, enclosures treated with 0.05 μg fenvalerate·L^{-1}, and an enclosure treated with the EC blank in 1984. Arrows indicate time of treatment. One standard deviation is presented on days with significant differences.

parameters monitored in the water column either within replicate enclosures or between treated enclosures and controls in a particular experiment, and therefore for brevity, these results are not shown. Solomon et al. (1985, 1986) and Shires (1983) observed similar results for the water chemistry of enclosures treated with permethrin, cypermethrin, and methoxychlor. This suggests that insecticides such as fenvalerate have little or no direct effects on water chemistry.

Effects of Fenvalerate on Density of Zooplankton

In 1983, statistical interpretation of the data was not possible. However, graphical representation of numbers of animals per litre over time suggests that 0.1 μg fenvalerate·L^{-1} caused a reduction in the densities of all the major groups of zooplankton with the exception of the rotifers (Fig. 2). In the case of the latter, number of animals per litre increased dramatically for approximately 3 wk following treatment. The time to recovery varied for each of the major groups. Nauplii appeared to recover most rapidly, with populations exceeding those of the control enclosure within 2 wk of treatment. The cladocerans and calanoids returned to levels similar to those in the controls by approximately 3 wk following treatment. The cyclopoids appeared to be the most sensitive and did not recover until approximately 5 wk post-treatment. The generation time for cyclopoids is longer than that of the cladocerans which may account for their apparent longer time to recovery.

In 1984, populations of cladocerans and nauplii were significantly reduced for approximately 3 and 1 wk, respectively, following treatment with 0.05 μg fenvalerate·L^{-1} (Fig. 3). The EC blank (Fig. 3) as well as the lower concentration of 0.01 μg·L^{-1} (Fig. 4) appeared to be non-toxic to these organisms. Populations of calanoids and cyclopoids were not significantly affected by either concentration of fenvalerate or the EC blank. As in 1983, populations of rotifers increased for approximately 3 wk in enclosures with mortality of cladocerans

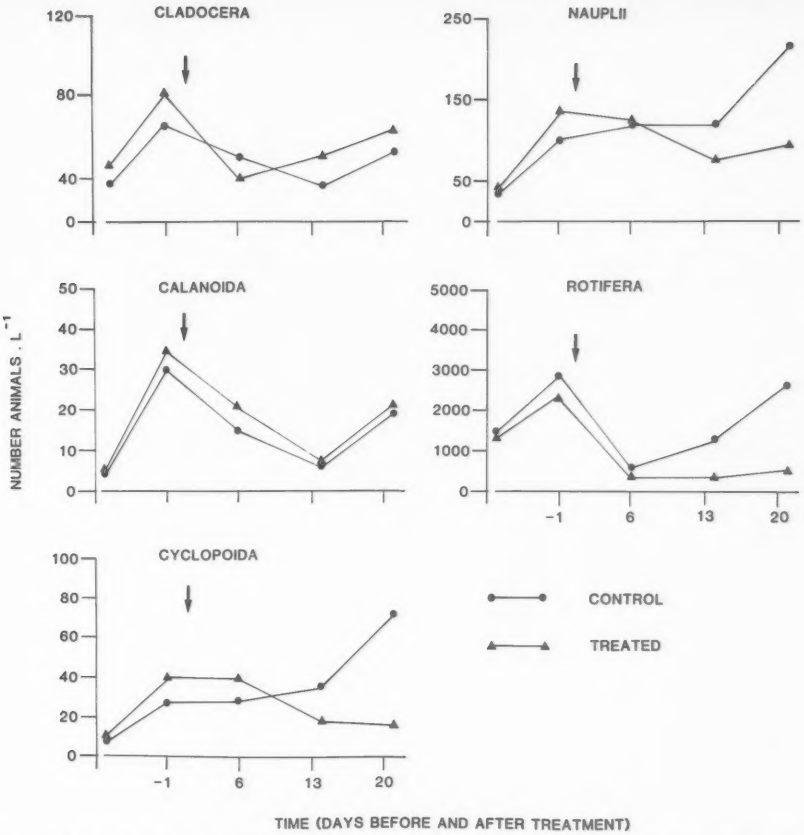

FIG. 4. Changes in mean densities of the major groups of zooplankton in control and fenvalerate-treated enclosures (0.01 $\mu g \cdot L^{-1}$) in 1984. Arrows indicate time of treatment.

(i.e. 0.05 μg fenvalerate$\cdot L^{-1}$). No such increase was observed on the three sampling dates following treatment with either 0.01 μg fenvalerate$\cdot L^{-1}$ (Fig. 4) or the EC blank.

Effect of Fenvalerate on Phytoplankton

The abundance of total phytoplankton (number per litre) was not affected by the treatment of the enclosure with 0.1 μg fenvalerate$\cdot L^{-1}$ when compared with the control enclosure (Fig. 5a). Total biomass of phytoplankton (milligrams per cubic metre) was lower in the treated enclosure from approximately 3 wk following treatment to the end of the sampling period (Fig. 5b). Relative biomass and numerical density of Chlorophyta increased following treatment (Fig. 6). This increase appeared to be at the expense of the Chrysophyta and the Cyanophyta which decreased in abundance following treatment.

Effect of Fenvalerate on Individual Rates of Filtration (FRs)

1983

The treatment of one enclosure with 0.1 μg fenvalerate$\cdot L^{-1}$ was acutely toxic to many species of zooplankton, and too few animals were obtained following treatment to allow regressions of filtering rate and body length (the accepted method for observing rates of filtration under natural conditions) (Chow-Fraser and Knoechel 1985). Instead, only data on FRs for species of a comparable size in both treated and control enclosures are presented.

At 15 d and 6 h before treatment, mean FRs of *Daphnia* spp., *C. lacustris*, and *D. oregonensis* varied between sampling dates but did not differ significantly between enclosures (Fig. 7). Treatment of the enclosure with 0.1 μg fenvalerate$\cdot L^{-1}$ caused an immediate (+6 h) decline in FRs of *Daphnia* spp. and, after a 24-h delay, a decline in the FRs of the other two species. Visual examination of the contents of the Haney chamber prior to emptying it indicated that live animals were present 1 d following treatment; however, FRs were close to zero at this time. FRs in the treated enclosure remained significantly below those of the control enclosure on days 4, 8, 21, and 58 following treatment. *Daphnia* spp. became rare in both control and treated enclosures approximately 1 mo following treatment.

1984

The measurements of FRs of different size classes of *Daphnia* spp. were combined from replicate enclosures to determine linear regressions of FRs versus body length (BL). The same procedure was followed for *C. lacustris*. The effects of fenvalerate on FRs were then determined by comparison of the slopes and intercepts of these regressions in treated and control enclosures. Although in situ samples were taken at two depths (1.5 and 3.0 m) in the water column, few animals were

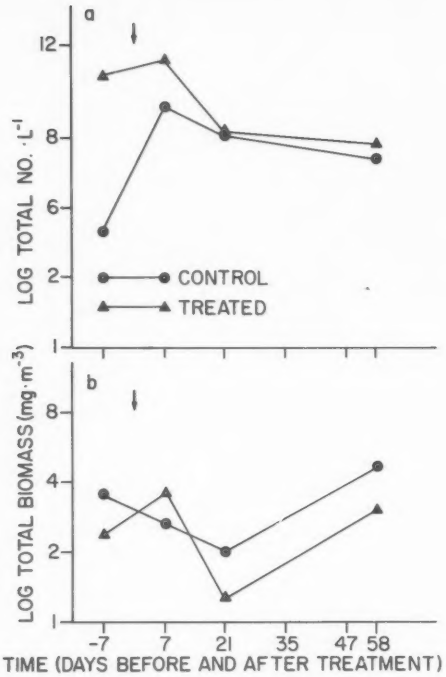

FIG. 5. Changes in (a) abundance and (b) biomass of total phytoplankton over time for a control enclosure and an enclosure treated with a nominal concentration of 0.1 μg fenvalerate·L^{-1} in 1983. Arrows indicate time of treatment.

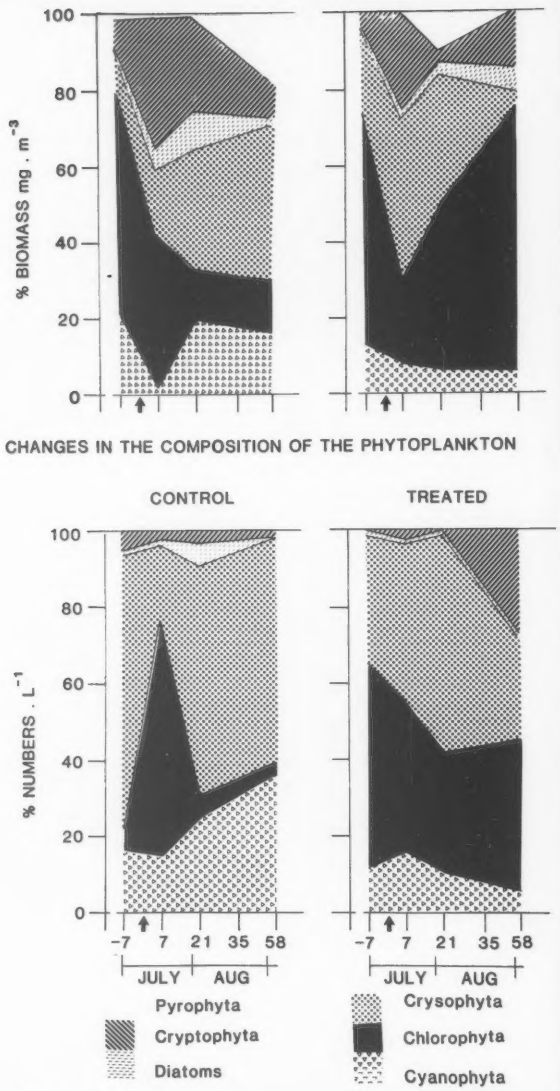

FIG. 6. Changes in (a) relative abundance and (b) biomass of the major groups of phytoplankton over time for a control enclosure and an enclosure treated with a nominal concentration of 0.1 μg fenvalerate·L^{-1} in 1983. Arrows indicate time of treatment.

obtained at 1.5 m. Similarly, not always enough animals were present in samples taken in the enclosure treated with the EC blank to obtain linear regressions. Therefore, data are presented only when animals were available in sufficient numbers and size classes for determining linear regressions.

Prior to treatment, regressions calculated for *Daphnia* spp. in the control, EC blank, and treated enclosures were not significantly different (Table 1; Fig. 8a, 8b). Treatment of enclosures with 0.05 μg fenvalerate·L^{-1} resulted in an immediate decrease in FRs at each depth in the water column (Table 1; Fig. 8c, 8d). Both the slope and the intercept of the regressions were significantly changed by the presence of the pesticide, suggesting that different sized organisms were not all equally affected. The decrease in FRs at 0.05 μg fenvalerate·L^{-1} was most apparent 1 d following treatment at both 1.5 and 3.0 m; several FRs were zero and no significant linear regression could be obtained. By day 6, however, FRs of animals in the treated enclosures at 3.0 m were not significantly different from those in the controls (Fig. 8e, 8f), indicating recovery from toxic stress. No animals were obtained at 1.5 m on this sampling date.

Regressions determined for FRs of *Daphnia* spp. exposed to 0.01 μg fenvalerate·L^{-1} were not significantly different from those of control animals following treatment (Table 1).

Lines of regression for the relationship between body size and filtering activity of *C. lacustris* at depths of 1.5 and 3.0 m in control enclosures and enclosures to be treated with the EC blank and 0.05 μg fenvalerate·L^{-1} were not significantly different (Table 2; Fig. 9a). Treatment with 0.05 μg fenvalerate·L^{-1} resulted in an immediate reduction in FRs at each depth in samples taken 0.5, 1, and 4 d following treatment (Table 2; Fig. 9b, 9c, 9d). By day 6, FRs of *C. lacustris* at 3.0 m were in the same range as those of the controls, although no significant regressions could be obtained on this treatment date for treated enclosures. The EC blank had no significant effect on linear regressions compared with those of the control enclosures.

Not enough animals were present in either control enclosures or enclosures treated with 0.01 μg fenvalerate·L^{-1} to determine FR–BL regressions, and therefore, data are expressed as a mean (±SD) FR for animals (size 0.45–0.60 mm) on a number of days pre- and post-treatment (Table 3). No significant effect of the pesticide was observed.

Prior to treatment, the FRs of adult female *D. oregonensis*

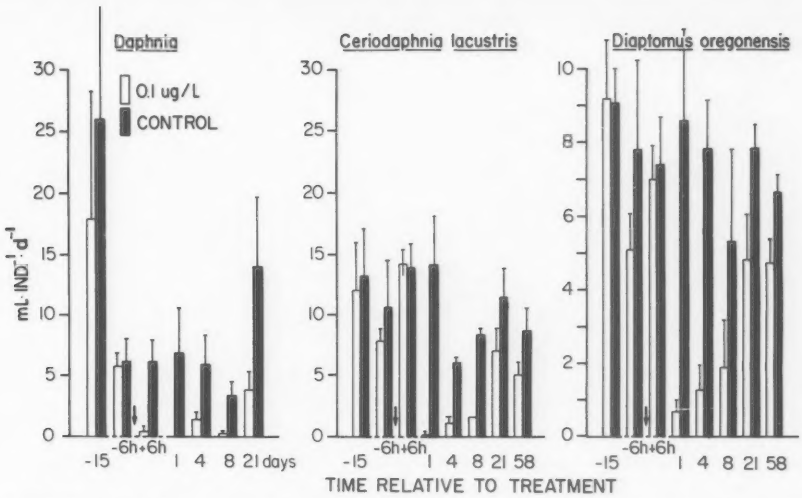

FIG. 7. Changes in the rates of filtration of *Daphnia* spp. *C. lacustris*, and *D. oregonensis* over time in a control enclosure and an enclosure treated with a nominal concentration of 0.1 μg fenvalerate·L^{-1} at 2.0 m in the water column.

were significantly different from those of the controls on −15 d in the enclosures to be treated with 0.05 μg fenvalerate·L^{-1} (Table 4). Treatment of enclosures with 0.05 μg fenvalerate·L^{-1} or with the EC blank did not significantly affect FRs of *D. oregonensis* with one exception. On 6 d following treatment with 0.05 μg fenvalerate·L^{-1}, FRs were significantly lower in treated enclosures than those in the control and EC blank enclosures. This may represent a delayed toxicological reaction to the pesticide but is more likely to reflect the large variation in natural filtration rates which sometimes occur (Haney 1985). A concentration of 0.01 μg fenvalerate·L^{-1} did not cause FRs to differ significantly from those of the controls (Table 5).

Effects of Fenvalerate on Community Rates of Filtration (CFRs)

CFRs were not measured in the preliminary experiment conducted during 1983. CFRs in 1984 were similar in all enclosures on pretreatment dates with two exceptions: on −1 d, the mean CFR in the >80 μm size fraction for enclosures to be treated with 0.05 μg fenvalerate·L^{-1} and sampled at 3.0 m in the water column was significantly higher than the corresponding mean CFR for the control enclosures (Fig. 10c). In addition, on −8 d, mean CFR of the >80 μm size fraction at 1.5 m in the enclosure to be treated with the EC blank was higher than the mean CFR in the control and treated enclosures (Fig. 10a). The direct effect of 0.05 μg fenvalerate·L^{-1} on CFRs was a significant reduction at both depths for the >80 μm size fraction of zooplankton (Fig. 10a, 10c). This reduction was apparent for two sampling dates following treatment, after which time, rates returned to levels similar to those of the controls. CFRs in the 30–80 μm size fraction of the zooplankton in the 0.05 μg fenvalerate·L^{-1} enclosures were not significantly different from those of the controls at 3.0 m in the water column (Fig. 10d). However, on day 14, CFRs in this size fraction at 1.5 m were significantly higher (Fig. 10b). The CFRs for zooplankton in the EC blank enclosure were more variable over the time of an experiment than the means of the CFRs in the control enclosures. However, no toxicity in the form of a reduction in CFR is indicated.

Treatment of enclosures with 0.01 μg fenvalerate·L^{-1} (Fig. 11) did not result in any significant changes in CFRs when compared with controls for either size fractions or depths, indicating no toxicity.

Discussion

Fenvalerate has been reported to have a half-life in natural waters of 6.3 to >14 d depending on the light conditions (Schimmel et al. 1983). The half-life of fenvalerate in this study was similar to that reported by Solomon et al. (1985) for permethrin in enclosures in Lake St. George (i.e. 2–4 d). The rapid dissipation of fenvalerate in lake water is probably due to microbial activity (Ohkawa et al. 1980; Miyamoto and Mikami 1982) as well as adsorption to sediment, suspended particulate matter, and the walls of the enclosures (Sharom and Solomon 1981; Muir et al. 1985).

Tagatz and Ivey (1981) found that the community structure of both laboratory and field estuarine benthic communities was altered at concentrations of fenvalerate as low as 0.1 μg·L^{-1}. Miura and Takahashi (1976) found that concentrations of 53 μg fenvalerate·L^{-1} in glass aquaria had no effect on copepods, but cladocerans were eliminated within 1–2 d post-treatment.

The relative insensitivity of populations of rotifers to pesticides, as indicated in the present study, has been shown in other studies (Miura and Takahashi 1976), and increases in populations in enclosures treated with insecticides have been reported elsewhere (Hurlbert et al. 1972; Papst and Boyer 1980). Kaushik et al. (1985) suggested that such increases in populations of rotifers are an indirect effect of the pesticide resulting from a release of the organisms from predation and competition due to removal of other species of zooplankton. This observation has been confirmed by Neill (1984) in freshwater in situ enclosures. Neill (1984) experimentally manipulated densities of cladocerans and copepods and produced highly significant increases in the biomass of rotifers. The increases occurred only when *Daphnia* were removed but not under copepod removal, which suggests that competition rather than predation was the

TABLE 1. Regression lines for the relationahip log FR vs. log BL of *Daphnia* spp. in co

Depth (m)	Treatment	D −8	−1
1.5	Control	$Y = 0.74 + 2.45\,X$ ($r^2 = 0.65$; $P = 0.05$)	$Y = 0.73 + 2.56\,X$ ($r^2 = 0.80$; $P = 0.05$)
1.5	0.05 μg fenvalerate·L^{-1}	$Y = 0.78 + 2.16\,X$ ($r^2 = 0.99$; $P = 0.05$)	$Y = 0.73 + 2.60\,X$ ($r^2 = 0.55$; $P = 0.05$)
1.5	EC	$Y = 0.36 + 0.96\,X$ ($r^2 = 0.86$; NS)	—
3.0	Control	$Y = 0.51 + 1.52\,X$ ($r^2 = 0.58$; $P = 0.001$)	$Y = 0.74 + 2.14\,X$ ($r^2 = 0.92$; $P = 0.05$)
3.0	0.05 μg fenvalerate·L^{-1}	$Y = 0.44 + 1.50\,X$ ($r^2 = 0.56$; $P = 0.05$)	$Y = 0.70 + 2.25\,X$ ($r^2 = 0.86$; $P = 0.01$)
3.0	EC	$Y = 0.63 + 2.57\,X$ ($r^2 = 0.91$; $P = 0.05$)	$Y = 0.47 + 1.00\,X$ ($r^2 = 0.16$; NS)
3.0	Control	—	$Y = 0.41 + 1.45\,X$ ($r^2 = 0.67$; $P = 0.01$)
3.0	0.01 μg fenvalerate·L^{-1}	—	$Y = 0.31 + 0.79\,X$ ($r^2 = 0.39$; NS)

TABLE 2. Regression lines for the relationship log FR vs. log BL of *C.*

Depth (m)	Treatment	−1	+0.5
1.5	Control	$Y = 0.96 + 1.32\,X$ ($r^2 = 0.90$; $P = 0.05$)	$Y = 1.27 + 2$ ($r^2 = 0.73$; $P =$
1.5	0.05 μg fenvalerate·L^{-1}	$Y = 1.32 + 1.83\,X$ ($r^2 = 0.99$; $P = 0.05$)	$Y = 1.22 + 5$ ($r^2 = 0.69$; $P =$
1.5	EC	—	$Y = 1.13 + 1$ ($r^2 = 0.97$; $P =$
3.0	Control	$Y = 0.93 + 1.32\,X$ ($r^2 = 0.71$; $P = 0.01$)	$Y = 1.25 + 1$ ($r^2 = 0.77$; $P =$
3.0	0.05 μg fenvalerate·L^{-1}	$Y = 1.16 + 2.00\,X$ ($r^2 = 0.77$; $P = 0.05$)	$Y = 0.86 + 2$ ($r^2 = 0.35$; $P =$
3.0	EC	—	—

pp. in control and treated enclosures at two depths.

	Days before and after treatment			
	+0.5	+1	+6	+13
56 *X* 0.05)	$Y = 0.96 + 2.82\,X$ ($r^2 = 0.74$; $P = 0.001$)	$Y = 0.65 + 2.25\,X$ ($r^2 = 0.56$; $P = 0.05$)	—	—
60 *X* 0.05)	$Y = 0.44 + 3.76\,X$ ($r^2 = 0.61$; $P = 0.01$)	No regression	—	—
	$Y = 0.99 + 3.06\,X$ ($r^2 = 0.86$; $P = 0.05$)	—	—	—
14 *X* 0.05)	$Y = 0.99 + 2.46\,X$ ($r^2 = 0.64$; $P = 0.001$)	$Y = 0.72 + 2.48\,X$ ($r^2 = 0.64$; $P = 0.01$)	$Y = 0.69 + 2.31\,X$ ($r^2 = 0.75$; $P = 0.001$)	$Y = 0.54 + 1.26\,X$ ($r^2 = 0.77$; NS)
25 *X* 0.01)	$Y = 0.54 + 1.84\,X$ ($r^2 = 0.37$; NS)	No regression	$Y = 0.68 + 4.37\,X$ ($r^2 = 0.63$; $P = 0.01$)	$Y = 0.88 + 3.39\,X$ ($r^2 = 0.70$; $P = 0.05$)
00 *X*	$Y = 0.94 + 3.39\,X$ ($r^2 = 0.92$; $P = 0.05$)	$Y = 0.53 + 3.11\,X$ ($r^2 = 0.79$; $P = 0.05$)	—	—
45 *X* 0.01)	$Y = 0.68 + 1.93\,X$ ($r^2 = 0.64$; $P = 0.05$)	$Y = 0.19 + 1.37\,X$ ($r^2 = 0.39$; NS)	$Y = 0.60 + 2.88\,X$ ($r^2 = 0.99$; $P = 0.05$)	$Y = 0.56 + 2.01\,X$ ($r^2 = 0.66$; $P = 0.05$)
79 *X*	$Y = 0.58 + 1.51\,X$ ($r^2 = 0.50$; $P = 0.05$)	$Y = 0.29 + 1.43\,X$ ($r^2 = 0.51$; $P = 0.01$)	$Y = 0.60 + 2.57\,X$ ($r^2 = 0.75$; $P = 0.01$)	$Y = 0.48 + 2.06\,X$ ($r^2 = 0.83$; $P + 0.01$)

L of *C. lacustris* in control and treated enclosures at two depths.

	Days before and after treatment		
+0.5	+1	+4	+6
1.27 + 2.14 *X* 0.73; $P = 0.01$)	$Y = 1.17 + 2.43\,X$ ($r^2 = 0.78$; $P = 0.05$)	$Y = 0.98 + 1.68\,X$ ($r^2 = 0.70$; $P = 0.01$)	—
1.22 + 5.24 *X* 0.69; $P = 0.01$)	No regression	No regression	—
1.13 + 1.84 *X* 0.97; $P = 0.10$)	$Y = 1.24 + 2.52\,X$ ($r^2 = 0.70$; $P = 0.01$)	$Y = 1.26 + 2.52\,X$ ($r^2 = 0.97$; $P = 0.05$)	—
1.25 + 1.94 *X* 0.77; $P = 0.01$)	$Y = 0.93 + 1.93\,X$ ($r^2 = 0.70$; $P = 0.01$)	—	$Y = 1.28 + 2.48\,X$ ($r^2 = 0.89$; $P = 0.001$)
0.86 + 2.76 *X* 0.35; $P = 0.1$)	No regression	—	No regression
—	$Y = 1.26 + 2.48\,X$ ($r^2 = 0.89$; $P = 0.001$)	—	—

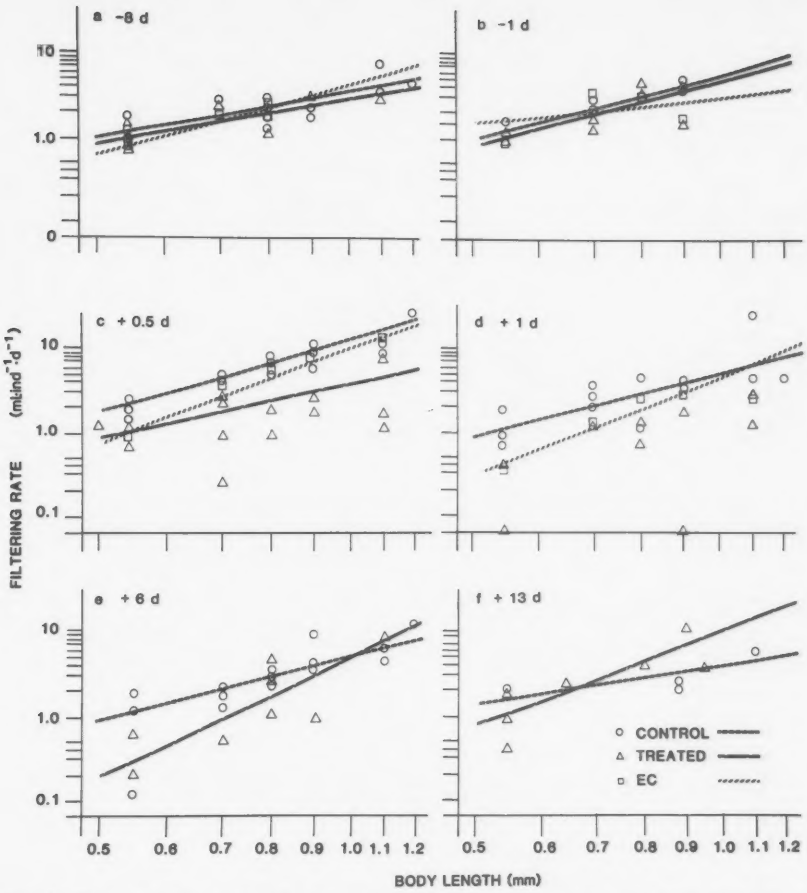

FIG. 8. Changes in the relationship of filtering rate (FR) and body length (BL) of *Daphnia* spp. in control enclosures, enclosures treated with a nominal concentration of 0.5 μg fenvalerate·L^{-1}, and an enclosure treated with the EC blank at 3.0 m in the water column. Lines drawn through the points represent a least squares fit to the data in the form log FR vs. log BL.

TABLE 3. Filtering rates of *C. lacustris* (mL·ind^{-1}·d^{-1}) in enclosures treated with 0.01 μg fenvalerate·L^{-1} and in untreated enclosures (at 3.0 m).

Date	Days before and after treatment	Treated enclosures (±SD)	Control enclosures (±SD)
July 12	−7	1.42 ± 0.96	0.69 ± 0.54
July 17	−1	1.24 ± 0.55	1.41 ± 0.36
July 18–19 (night)	+0.5	1.23 ± 0.29	1.40 ± 0.56
July 19	+1	1.17 ± 0.72	1.28 ± 0.23
July 21	+3	1.09 ± 0.60	1.05 ± 0.49
July 31	+13	0.99 ± 0.27	1.28 ± 0.49

major influencing factor. The present study also confirms these findings.

The changes in the abundance of the major phytoplankton groups are probably not due to the direct toxic effect of fenvalerate for the following reasons: (1) they began to occur approximately 3 wk following treatment when the concentration of the pesticide was extremely low and (2) the synthetic pyrethoids have been reported to be toxic to algae only at 1 000–10 000 times the concentrations applied in our study (Stratton and Corke 1982). The effects can instead be attributed indirectly to the pesticide. Grazing is thought to be one of several environmental factors which can influence the growth of natural populations of phytoplankton (Frost 1980), and several studies have suggested that filter-feeding zooplankton, especially cladocerans, have a significant impact on the abundance of phytoplankton, especially the small, edible, high-quality nanoplankton (Porter 1973; Gliwicz 1975; Lynch 1978). Several researchers have suggested that increases in phytoplankton should occur in aquatic ecosystems after the removal of the filter-feeding zooplankton by a toxicant (Hurlbert 1975; Papst and Boyer 1980). Treatment of an enclosure with 0.1 μg fenvalerate·L^{-1} caused an immediate reduction in the large, filter-feeding zooplankton for a period of approximately 3 wk. This coincides with the period when the Chlorophyta began to increase in density. The composition of the Chlorophyta during this period consisted of small, readily digestible green algae

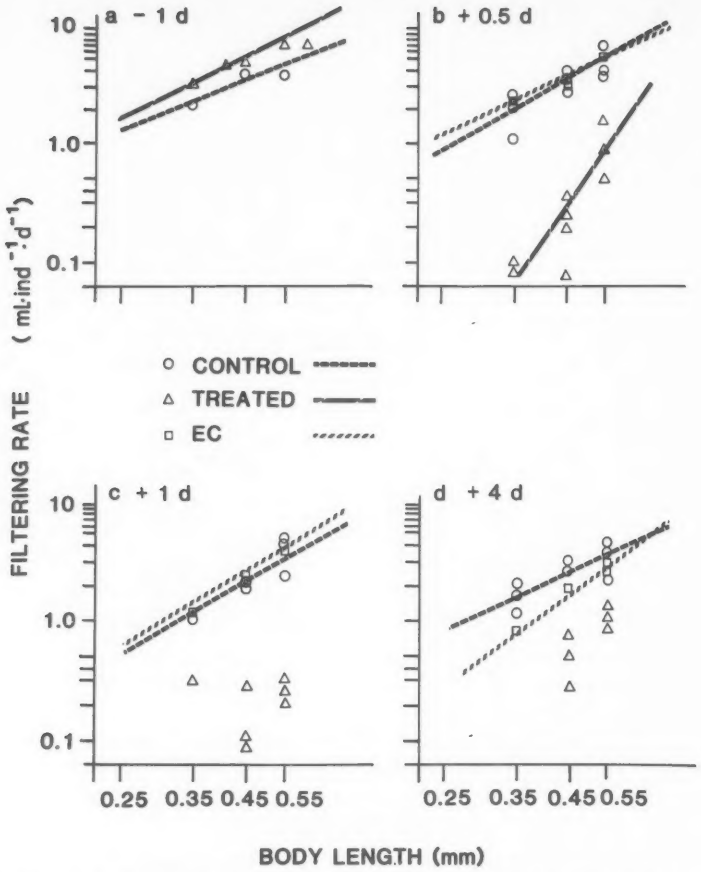

FIG. 9. Changes in the relationship of filtering rate (FR) and body length (BL) of *C. lacustris* in control enclosures, enclosures treated with a nominal concentration of 0.05 μg fenvalerate·L^{-1}, and an enclosure treated with the EC blank at 1.5 m in the water column. Lines drawn through the points represent a least squares fit to the data in the form of FR vs. log BL.

TABLE 4. Filtering rates of *D. oregonensis* (mL·ind^{-1}·d^{-1}) in untreated enclosures and enclosures treated with 0.05 μg fenvalerate·L^{-1} and in an EC blank equivalent to 0.05 μg fenvalerate·L^{-1} (at 3.0 m).

Date	Days before and after treatment	Treated enclosures (±SD)	Control enclosures (±SD)	EC blank enclosures (±SD)
June 12	−15	2.58 ± 0.63[a]	4.06 ± 0.72	2.62[b]
June 19	−1	4.47 ± 3.99	4.11 ± 1.48	—[c]
June 20–21 (night)	+0.5	5.46 ± 0.16	5.96 ± 2.40	7.03 ± 0.62
June 22	+1	2.16 ± 0.78	4.68 ± 2.42	3.12 ± 0.32
June 26	+4	3.17 ± 1.24	4.10 ± 0.97	3.08 ± 1.34
July 3	+6	2.14 ± 0.86[a]	5.49 ± 1.40	6.88 ± 2.20
July 18	+21	3.99 ± 2.13	4.23 ± 1.46	2.56 ± 0.85

[a]Significantly different from controls.
[b]Only one animal available for measurement.
[c]No animals available.

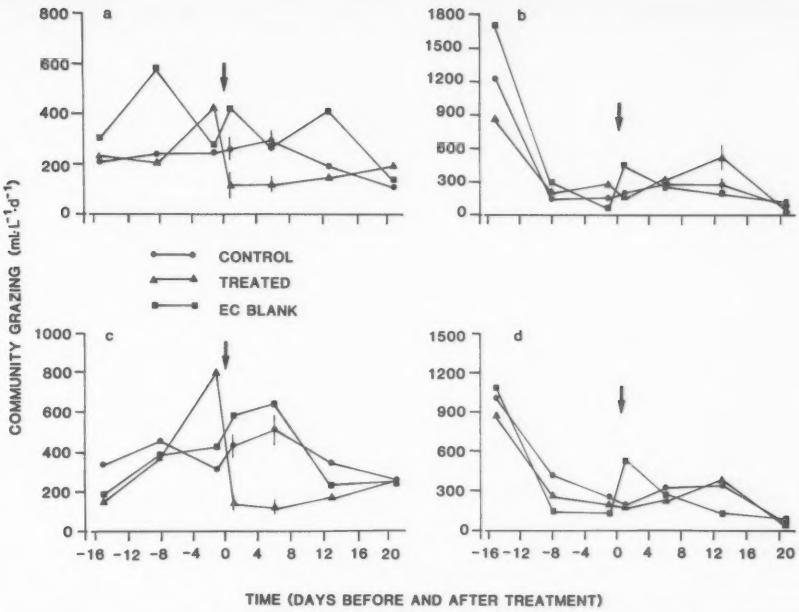

FIG. 10. Mean changes in rates of community grazing over time in control enclosures, enclosures treated with a nominal concentration of 0.05 μg fenvalerate·L^{-1}, and an enclosure treated with the EC blank. (a) Size fraction >80 μm at 1.5 m in water column; (b) size fraction 30–80 μm at 1.5 m in water column; (c) size fraction >80 μm at 3.0 m in water column; (d) size fraction 30–80 μm at 3 m in water column. One standard deviation is presented on days with significant differences. Arrows indicate time of treatment.

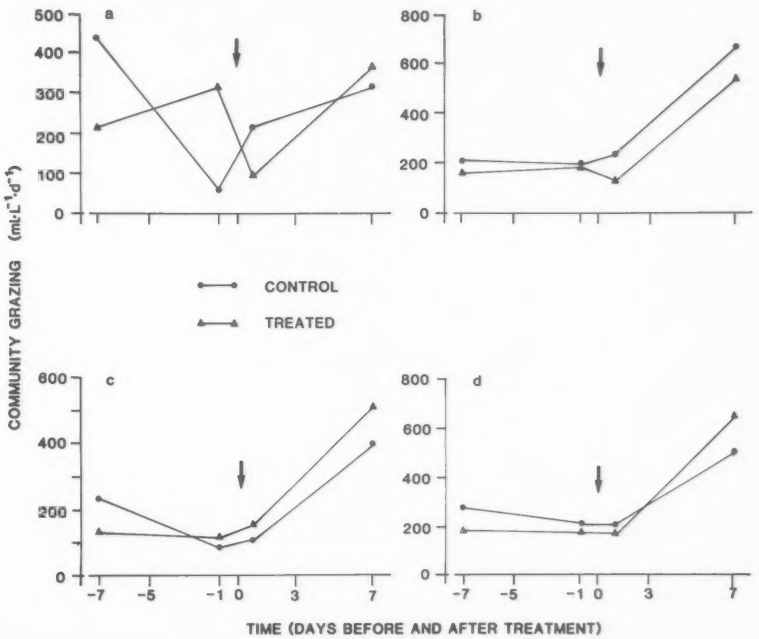

FIG. 11. Mean changes in rates of community grazing over time in control enclosures and enclosures treated with a nominal concentration of 0.01 μg fenvalerate·L^{-1}. (a) Size fraction >80 μm at 1.5 m in water column; (b) size fraction 30–80 μm at 1.5 m in water column; (c) size fraction >80 μm at 3.0 m in water column; (d) size fraction 30–80 μm at 3 m in water column. Arrows indicate time of treatment.

TABLE 5. Filtering rates of *D. oregonensis* ($mL \cdot ind^{-1} \cdot d^{-1}$) in enclosures treated with 0.01 μg fenvalerate·L^{-1} and in untreated enclosures (at 3.0 m).

Date	Days before and after treatment	Treated enclosures (±SD)	Control enclosures (±SD)
July 17	−1	3.52 ± 0.71	3.70[a]
July 18–19 (night)	+0.5	3.11 ± 0.56	3.16 ± 1.19
July 19	+1	2.78 ± 0.96	2.61 ± 0.85
July 21	+3	1.53 ± 1.16	1.02 ± 1.10
July 24	+6	1.62 ± 1.10	1.48 ± 1.06
July 31	+13	3.30 ± 0.40	3.13 ± 0.87

[a]Only one animal available.

such as *Ankistrodesmus falcatus*, *Cosmarium* sp., *Chlamydomonas* sp., etc., all species which are likely to form a large percent of the diet of herbivorous zooplankton (Porter 1973, 1975; Thompson et al. 1982; Ferguson et al. 1982; DeMott 1983). Therefore, the increase in the Chlorophyta may be attributed to the removal of the large grazers. This indirect effect of the pesticide occurs long after (21–54 d) the direct toxic effect of the pesticide has disappeared. This type of response has been observed in other experimental enclosures (Parsons 1978; Menzel and Case 1977; Thomas et al. 1977) and illustrates another advantage in using large-volume in situ enclosures to evaluate pesticide toxicity.

FRs measured for all three species prior to the treatment of the enclosures and in the control enclosures were quite variable but were in the range of rates reported for the same species in several southern Ontario lakes (Haney 1973; Chow-Fraser and Knoechel 1985; Chow-Fraser 1986; Knoechel and Holtby 1986). Regression slopes for the relationship between FR and BL for the cladocerans ranged from 0.79 to 2.82 in our study. Haney (1985) observed that daytime regressions for FRs of *Daphnia* spp. were characterized by low intercept values, low regression slopes (1.27–1.80), and correlation coefficients that are generally not significant. In their attempt to model in situ rates of filtration of cladocerans, Chow-Fraser and Knoechel (1985) reported slopes of the regression from 2.45 to 3.19. Knoechel and Holtby (1986) studied filtration rates of zooplankton in Lake St. George and predicted a regression slope of 2.48 as a function of size. *Diaptomus oregonensis* was assigned a mean individual grazing rate of 2 $mL \cdot ind^{-1} \cdot d^{-1}$ by these same authors. These data suggest that the filter-feeding behaviour of the organisms sampled before treatment and in controls probably represents the normal feeding behaviour of the organisms at this time of year.

The measurement of FRs for species of zooplankton exposed to a contaminant under field conditions is rare. Cooley (1977) reported a 72% drop in filter-feeding performance for *D. retrocurva* filter-feeding near a canal discharging pulp mill effluent. Gliwicz (1977) observed a severe depression of the filtration rates of zooplankton in a eutrophic lake during the summer when the biomass of blue-green algae was high. Some species of blue-green algae, e.g. *Anabaena* spp., have been reported to contain a toxin which is known to cause reductions in the filtration rates of *Daphnia* (Crowley 1973; Arnold 1971). Lampert (1982) found that *Daphnia* responded very quickly to the presence or absence of a toxin produced by the blue-green algae, *Microcystis aeruginosa*, and attributed this to discrimination on the basis of taste. Taste discrimination is not likely the cause of a drop in rates of filtration in the present study. Synthetic pyrethroids such as fenvalerate are thought to affect the nervous system of arthropods (Miller and Adams 1982). The filtration and ingestion of food by filter-feeding zooplankton requires movement of appendages and therefore coordination of the nervous system. A reduction in rates of filtration by zooplankton exposed to fenvalerate likely indicates a direct toxic effect of the pesticide on the nervous system.

FRs can be affected by a number of intrinsic and extrinsic factors other than inhibition by toxic substances. Of these factors, the concentration of food present in the water has been shown to have a significant effect on FRs (Burns and Rigler 1967). Food concentrations greater than a critical concentration (the incipient limiting level) can cause a decline in the filtering rate. FRs in the enclosure treated with 0.1 μg fenvalerate·L^{-1} were significantly lower than those of the control approximately 2 mo following treatment, and this may be an indirect effect of the pesticide due to an increase in the number of edible algal cells. The increase in Chlorophyta may have reduced the FRs of organisms which remained in low numbers following treatment or recolonized the enclosure at a later date.

The CFRs measured in the control enclosures and enclosures prior to treatment with fenvalerate are in the same range as those reported by Haney (1973) and Lampert and Taylor (1985) for a similar time of year (i.e. 200–1 800 $mL \cdot L^{-1} \cdot d^{1}$). This suggests that the CFRs measured in our study are representative of normal CFRs. Filtration rates of zooplankton communities as measured using the Haney chamber are partially a consequence of the abundance of zooplankton trapped within the chamber when the doors are closed and partially due to actual rates of filtration of individual species (Haney 1973). This is one explanation for the variability of CFRs measured in ecological studies (Lampert and Taylor 1985). The density of animals within the chamber is also an important factor to consider when CFRs are used as an index of toxicity. The decrease in CFRs after treatment of enclosures with 0.05 μg fenvalerate·L^{-1} can be attributed not only to a reduction in the densities of the large herbivorous, filter-feeding cladocerans but also to reductions in FRs as noted above. Similarly, increases in CFRs can be attributed to the densities of organisms in the chamber. The 30–80 μg fraction of the zooplankton contains mostly rotifers, with some nauplii and very small *Bosmina* (K. E. Day, pers. obs.). The increase in density of the rotifers following treatment coincides with the increase in CFRs for this size fraction at 1.5 m. FRs of *Keratella* and *Polyarthra* have been reported to range from 24 to 216 $\mu g \cdot ind^{-1} \cdot d^{-1}$ (Bogdan and Gilbert 1982). Populations of rotifers of approximately 2000 $ind \cdot L^{-1}$ in treated enclosures (14 d following treatment) would therefore be expected to filter 48–432 $mL \cdot L^{-1} \cdot d^{-1}$, an amount similar to the rates reported 2 wk following treatment. The filtration rates of the 30–80 μg size fraction did not increase at 3.0 m. This can be explained by the distribution of rotifers in the water column. Neill (1984) found that *Keratella* spp. were most abundant at 0–2 m during June and July. Rotifers were not sampled at different depths in the present study, but *Keratella* spp. were largely responsible for the large increase in numbers of rotifers following treatment. The depth distribution of these organisms as noted by Neill (1984) would explain why CFRs increased at 1.5 m but not at 3.0 m.

The measurement of changes in CFRs and FRs was a more rapid index of toxicity and of equal or greater sensitivity than monitoring changes in the densities of populations. Data using

either CFRs or densities of the populations would indicate toxicity to communities at 0.05 μg fenvalerate·L^{-1} and no effect at 0.01 μg fenvalerate·L^{-1}.

The consequences of a decrease in rates of filtration by organisms exposed to a toxicant may be twofold. First, the inhalant current produced by movement of the thoracic appendages subserves respiration as well as feeding in filter-feeding zooplankton (Berman and Heinle 1980), and it is essential that filtration continues even if food is not being collected. Second, there is a threshold concentration of food that must be ingested for an individual to maintain its basic metabolic needs (Lampert 1977). This threshold value is the absolute minimum food concentration at which the individual organism can live. Similarly, there is a threshold concentration of food for the population which is higher than the individual threshold in order to compensate for losses of biomass (mortality) (Lampert 1977). If toxic substances have an inhibitory effect on rates of filtration but not respiration, the threshold concentration will shift to a higher value. Kersting (1983) found that the concentration of *Chlorella* at which a population of *D. magna* could survive shifted from 7×10^5 to 1×10^7 μm^3·mL^{-1} as a consequence of pesticide toxicity. The overall conclusion is that populations exposed to a toxicant may not be able to survive at low natural food concentrations in the presence of a contaminant.

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Coastal Upwelling and *Oikopleura* Occurrence ("Slub"): A Model and Potential Application to Inshore Fisheries

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Variations in the occurrence of *Oikopleura* spp. were strongly linked to the wind field and ensuing water temperatures in an inshore region of eastern Newfoundland during June–August of 1979 and 1981–83. *Oikopleura* foul inshore fishing gear with their discarded houses ("slub") and fluctuate in abundance from day to day as a function of wind-driven upwelling. Densities of *Oikopleura* in cold upwelling water during four years ranged between 20 and 800/m^3. *Oikopleura* densities <1/m^3 occurred when upwelling ceased and warmer water occupied the inshore region. A simple model incorporating a daily averaged wind vector, Julian day, and growing degree-day explained 62% of the daily variation in *Oikopleura* abundance in 1979. The model yielded density estimates that were significantly ($p<0.05$) correlated with observed densities in each of the other three years. We provide evidence that net fouling by *Oikopleura* in the inshore and maximum Atlantic cod (*Gadus morhua*) catch is coincident and suggest that an annual hindcast index of slub intensity may help determine the impact of slub conditions on the inshore fishery.

De juin à août 1979 et 1981–1983, les variations de la fréquence de *Oikopleura* spp. étaient fortement liées à la vitesse du vent et à la température de l'eau dans une région côtière de l'est de Terre-Neuve. Les cocons abandonnés de *Oikopleura* encrassent les engins de pêche côtière; l'abondance de cet organisme fluctue d'une journée à l'autre en fonction des remontées d'eaux profondes entraînées par le vent. Dans les eaux froides de remontées profondes, les densités de *Oikopleura* ont varié de 20 à 800/m^3 pendant quatre années. Des densités inférieures à 1/m^3 ont été observées quand les remontées d'eaux profondes ont cessé et que des eaux plus chaudes baignaient la région côtière. Un modèle simple portant sur un vecteur moyen quotidien du vent, le jour Julien et le degré-jour de croissance a expliqué 62% de la variation quotidienne de l'abondance de *Oikopleura* en 1979. Le modèle a généré des estimations de la densité qui étaient corrélées de façon significative ($p<0,05$) avec les densités observées au cours des trois autres années. Nous présentons des preuves à l'effet que la salissure des filets côtiers par *Oikopleura* et les prises maximum de morue de l'Atlantique (*Gadus morhua*) coïncident; de plus, nous formulons l'hypothèse qu'un indice annuel de l'intensité des salissures pourrait servir à déterminer l'incidence de celles-ci sur la pêche côtière.

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The mucous houses of *Oikopleura* spp. (Tunicata: Appendicularia) are responsible for the "slime" or "slub" (as it is termed in Nova Scotia and Newfoundland, respectively) that fouls the trap and gill nets of inshore fishermen in the Northwest Atlantic region (Buggeln 1978, 1980; Mahoney and Buggeln 1983; Deibel 1987). The relatively large (6–40 mm) (Alldredge 1976; Deibel 1978) houses of *Oikopleura* are produced at a maximum rate of between 6 and 8/day by an individual larvacean (Lohmann 1909; Barnes 1974; Hamner et al. 1975) and readily accumulate on fishing nets set for Atlantic cod (*Gadus morhua*) and Atlantic salmon (*Salmo salar*) (Buggeln 1980; Mahoney and Buggeln 1983; Deibel 1987). It is supposed that *Oikopleura* fouling reduces the efficiency of nets. The houses and associated particulates (e.g. phytoplankton, microzooplankton, fecal pellets, detritus, etc.) (Alldredge 1976) make nets more visible and they are presumably avoided by fish (Diebel 1987). Nets must be frequently hauled for cleaning, resulting in reduced fishing effort and catch (Mahoney and Buggeln 1983; Lear et al. 1986). Net fouling by *Oikopleura* is a serious problem: it has drawn considerable media attention (Buggeln 1980; Lear et al. 1986), methods of cleaning and treating nets have been systematically investigated (Buggeln 1978; Deibel 1987), and a recent report on the factors affecting the inshore cod fishery highlighted *Oikopleura* as a contributing factor to reduced fishing efficiency, effort, and catch (Lear et al. 1986).

Fishermen are aware of the conditions leading to slub and agree that it is most apparent under wind conditions coincident with the appearance of cold, clear water (Buggeln 1978, 1980).

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Several authors attest the observations made by fishermen and suggest that the occurrence of slub is a function of variations in the wind, current, and tide which result in cold water masses, laden with *Oikopleura*, invading the inshore (Buggeln 1978; Lear et al. 1986). In support of this explanation the two most common species of *Oikopleura* in the Northwest Atlantic (*O. vanhoeffeni* and *O. labradoriensis*) are cold-water inhabitants (Udvardy 1954; Bückmann 1970), their houses are extremely adhesive to fishing net material (Mahoney and Buggeln 1983), and *O. vanhoeffeni* is one of the largest species (Diebel et al. 1985).

Recent work by Frank and Leggett (1981, 1982) and Taggart and Leggett (1987) demonstrated that the water mass and plankton community dynamics in the inshore zone of eastern Newfoundland are intimately tied to variations in the wind field on the scale of 2–6 d, a result consistent with Templeman's (1966) wind-driven water mass exchange hypothesis. The predominant effect of wind forcing in this region is the periodic upwelling of cold subthermocline water in the inshore and an accompanying change in composition of the plankton community. As *O. vanhoeffeni* and *O. labradoriensis* are cold-water inhabitants, and as slub is a periodic phenomenon apparently related to meteorological and water mass dynamics, we hypothesized that oscillations in the occurrence of *Oikopleura* in the inshore would be a predictable function of wind.

In this paper we examine the relationship between variation in the occurrence of *Oikopleura* in the inshore waters of eastern Newfoundland and variation in meteorological and hydrographic data. A simple model is derived and tested using three independent data sets. We explore the potential of the model for addressing problems in the inshore fishery.

Methods

Data Sources

Oikopleura spp. were collected during the summers of 1979 and 1981–83 in the inshore region of Bryants Cove, Newfoundland (45°40.5′N, 53°11.0′W). In 1979, sample volumes of ~2 m^3 each were collected at a depth of 1 m almost daily from 12 June through 26 July at three sites immediately adjacent to the beach at the head of the cove with a 153-μm-mesh net mounted on a Plexiglas sled (Frank and Leggett 1981). During 1981–83 an 80-μm-mesh net and a high-volume pump (Taggart and Leggett 1984) were used to collect *Oikopleura*. Samples of 1–2 m^3 volume were taken from late June to early August (every 0.3–2 d) at as few as 7 and as many as 43 sites throughout the cove (Taggart and Leggett 1987). Sampling depth ranged from 0 to 9 m. All of the samples were preserved in 4% formalin–seawater buffered with sodium borate. *Oikopleura* were enumerated from all samples unless the number appeared >100 in which case subsamples were taken using the Huntsman Marine Laboratory "beaker" technique (Van Guelpen et al. 1982), and the total numbers were estimated.

Daily measurements of water temperature were taken in 1979 in the subtidal zone adjacent to the beach at Bryants Cove using a YSI thermistor probe. The only temperature records available during 1981 were those provided by S. Akenhead (Department of Fisheries and Oceans, St. John's, Nfld.) from a Ryan thermograph recording at 4-h intervals and located at 10 m depth in Harbour Grace, an embayment immediately adjacent (1.6 km) to Bryants Cove. We considered the data from Harbour Grace representative, as Leggett et al. (1984) have shown that at much larger scales, temperature variations along the entire east coast of Newfoundland are similar and synchronous. Temperature records for 1982–83 were obtained at 10-min intervals from an Aanderra RCM4 current meter moored at a depth of 4.5 m in the cove from June to August. Temperature data from 1982–83 were smoothed to hourly values using a standard narrow-band filter (Godin 1972) to remove high-frequency variations (<1 h) (see Taggart and Leggett 1987). Daily temperature records for 1979 and thermograph data for 1981 were not smoothed.

Hourly wind speed and direction and growing degree-day values (5°C baseline) measured at St. John's airport (located 33 km east of Bryants Cove) were obtained from monthly meteorological summaries (Environment Canada, Atmospheric Environment Service (AES)). Wind directions were rotated 180° to downwind and speed and direction were decomposed into offshore (U_w) and longshore (V_w) vectors resolved around 54° (the major axis offshore direction at Bryants Cove). These data were smoothed with a single pass of an hour-centred normally weighted 12-point moving average (Taggart and Leggett 1987).

Analysis

Multivariate linear regression was used to examine the relationship between *Oikopleura* abundance and a number of meteorological and hydrological variables. *Oikopleura* abundance was expressed as a daily geometric average ($\log_e$(no./m^3) + 1). This transformation was chosen to improve the skewed distribution of the data caused by the disproportionately large number of zero and near-zero abundance estimates. The independent variables included the water temperature at the time of sampling (or an average value if more than one measurement was made in one day), U_w averaged over 3, 6, 12, and 24 h immediately prior to sampling, the daily growing degree-day estimate, the daily cummulative growing degree-day estimate, and the Julian day. These variables were chosen a priori because (1) there was evidence that temperature and wind influence *Oikopleura* abundance (Udvardy 1954; Bückmann 1970; Buggeln 1978; Lear et al. 1986), (2) Julian day had the potential to account for the generally declining seasonal trends in *Oikopleura* abundance which have been reported in the literature (Mahoney and Buggeln 1983) and were apparent in our data, and (3) growing degree-day provides a surrogate measure of potential heat input to the water column and has been successfully used in modelling event timing and biological production in other aquatic systems (e.g. Burgner 1980; Colby and Nepszy 1981; Leggett et al. 1984).

Multivariate analysis was used to identify those variables which consistently explained the most variation in the *Oikopleura* abundance observed within and among years. Our quantitative selection criteria were the regression statistics r^2, Mallows *Cp* (Hocking 1976), and *F*-values. Once selected, the variables were used to model only the 1979 data. The 1979 data series was chosen to provide the model parameters because (1) it was a relatively long series, (2) it began earlier in the season than any of the other years, and (3) it displayed the greatest amount of variation in *Oikopleura* abundance. The resulting model was then tested independently on the 1981–83 data series. The goodness of fit between the observed values and those produced by the model for each year was assessed using parametric (Pearson) and rank (Spearman) correlation statistics.

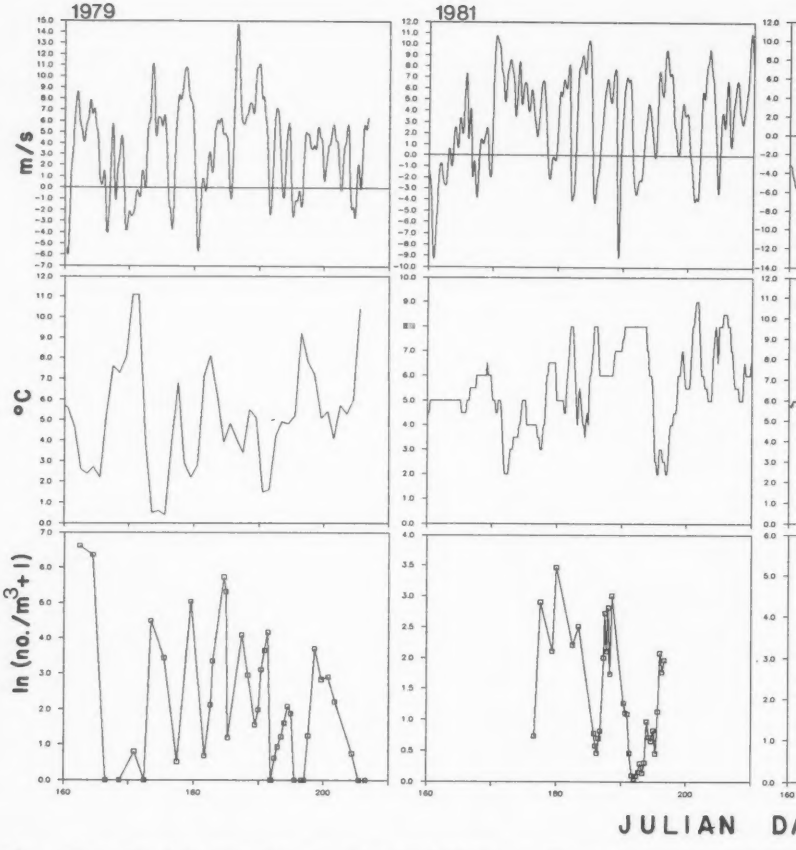
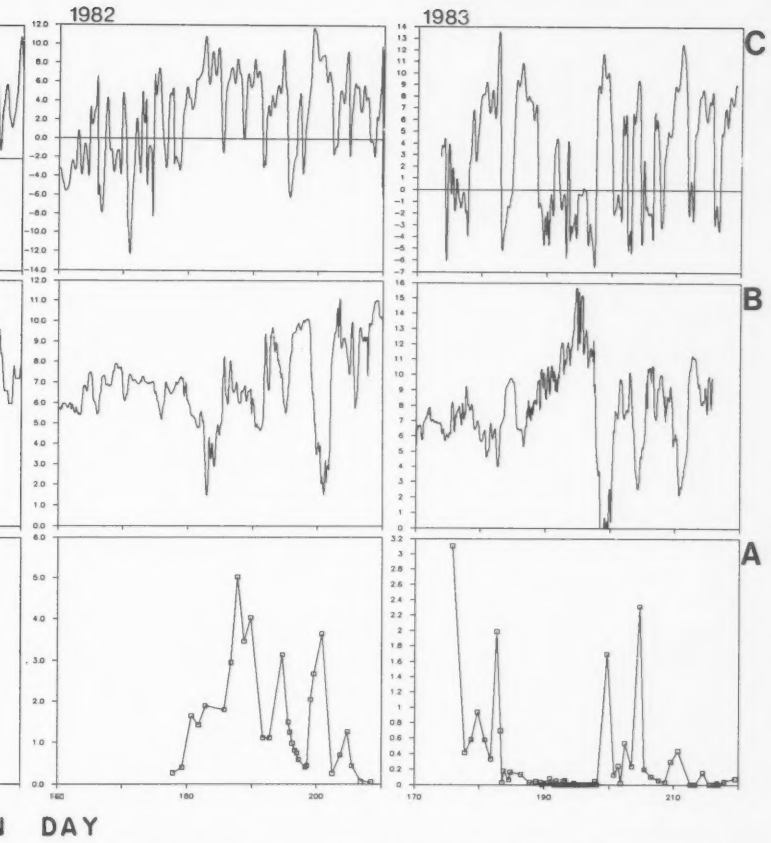


FIG. 1. Time series of (A) geometric-average density of *Oikopleura*, (B) water temperature, and (C) c
Note changes in scale among years for Fig. 1A, 1B, and 1C.



and (C) onshore–offshore wind component (U_w) in Bryants Cove in 1979, 1981, 1982, and 1983.

TABLE 1. Pearson correlation coefficients between the geometric average of *Oikopleura* density, water temperature, and the 24-h average of the *U*-component of wind (U_{w24}). Significance of correlation and sample size for each year and all years combined is provided.

Cross variables	1979	1981	1982	1983	All years
U_{w24}	−0.66	−0.56	−0.70	−0.61	−0.61
Temperature	0.0001	0.026	0.0001	0.0001	0.0001
	32	16	25	39	112
U_{w24}	0.74	0.39	0.61	0.30	0.49
Oikopleura	0.0001	0.132	0.0012	0.05	0.0001
	32	16	25	41	114
Temperature	−0.61	−0.39	−0.59	−0.43	−0.56
Oikopleura	0.0002	0.135	0.002	0.007	0.0001
	32	16	25	39	112

Results

Abundance estimates of *Oikopleura* in Bryants Cove exhibited extreme inter- and intra-annual variation (Fig. 1A). Maximum densities of *Oikopleura* during the four summers ranged between 20 and 800/m^3. Minimum densities were frequently <1/m^3. Within-year variation in *Oikopleura* abundance appeared on inspection to be inversely correlated with water temperature (Fig. 1B) and positively correlated with U_w (Fig. 1C). Periods of prolonged offshore wind (positive values of U_w) and sharply declining temperature, particularly in 1979 and 1981, were coincident with increased densities of *Oikopleura*. In contrast, periods of relatively weak offshore winds or prolonged onshore winds (negative values of U_w) resulted in increased temperature and decreased *Oikopleura* abundance. This was particularly evident between days 189 and 198, 1983 (8–17 July), when water temperature increased almost monotonically from 7 to ~16°C and there were virtually no *Oikoleura* in the water column (Fig. 1A).

The above observations are supported by significant inverse correlations between U_w averaged over 24 h (U_{w24}) and temperature in each year and for all years combined (Table 1). This result is consistent with the reciprocal relationship between wind stress and water temperature derived from spectral analysis techniques (Taggart and Leggett 1987). *Oikopleura* density was significantly and positively correlated with U_{w24} in three of the four years and for all years combined. *Oikopleura* was negatively correlated with temperature, a result that is consistent with reports from previous studies (see the introduction). U_{w24} exhibited the strongest correlation with both temperature and *Oikopleura* abundance among the four averages of U_w analysed (3, 6, 12, and 24 h).

Exploratory multivariate regression analysis revealed that U_{w24}, Julian day, and growing degree-day (all three were normally distributed and were readily available from monthly meteorological summaries) consistently provided the greatest amount of explained variation in the occurrence of *Oikopleura* in Bryants Cove both within and among years. U_{w24} alone explained the greatest amount of variation in four out of five analyses (1979, 1981, 1982, 1983, and all years combined). Temperature did not generally make a significant contribution to the explained variance due to its strong correlation with U_{w24} (Table 1). Julian day and growing degree-day each provided significant contributions to the explained variance in three out of the five analyses.

Fitting the three variables to the 1979 data set yielded the following model which explained 62% ($p < 0.0001$) of the total variation in *Oikopleura* abundance (Fig. 2A).

$$(1)\quad \textit{Oikopleura} = 0.421\ U_{w24} + 0.067\text{GDD} - 0.041\text{JD} + 7.775$$

where *Oikopleura* density was expressed as $\log_e$ (no./m^3 + 1), GDD was the daily growing degree-day, and JD was the Julian day. The model was judged statistically sound because the independent variables and their parameter estimates were not correlated ($\alpha = 0.05$), colinearity among the independent variables was not evident (diagnostic procedure of Belsley et al. 1980), and the error estimates were not autocorrelated (Durbin-Watson two-tailed d statistic, $\alpha = 0.05$, Draper and Smith 1980).

When the model parameters were applied to the 1981–83 data the output reproduced the observed oscillations of *Oikopleura* in each year (Fig. 2B, 2C, 2D). Variations in amplitude were also reflected by the model for all years except 1983 (Fig. 2D). The parametric and nonparametric correlation coefficients between the observed and modelled *Oikopleura* densities were significant in all cases ($p \leq 0.05$), although not surprisingly weakest in 1983 (Table 2). The overall significance of fit of the model in the three independent tests using the combined probability test (Sokal and Rohlf 1969) was $p < 0.00004$.

Discussion

The Model

The simple empirical model (eq. 1) not only reproduced major oscillations in the occurrence of *Oikopleura* in Bryants Cove, it also provided statistically significant estimates of *Oikopleura* density in all years tested. We believe that this resulted mainly because the wind field is an excellent predictor of the physical (e.g. temperature, salinity, currents) and biological (e.g. capelin larvae, micro- and macro-zooplankton, gelatinous zooplankton, etc.) characteristics of water masses in the inshore (Taggart 1986; Taggart and Leggett 1987; Frank and Leggett 1981, 1982) and because *Oikopleura* is an indicator of water mass type (Udvardy 1954; Bückmann 1970). The fact that U_{w24} was the dominant variable confirms the observation by fishermen that slub conditions are most severe during periods of upwelling favourable winds, no matter what geographic location is considered (Buggeln 1978, 1980). Nevertheless, it is important to recognize that the wind variable (U_{w24}) in the model is site specific. It is doubtful that the offshore orientation used

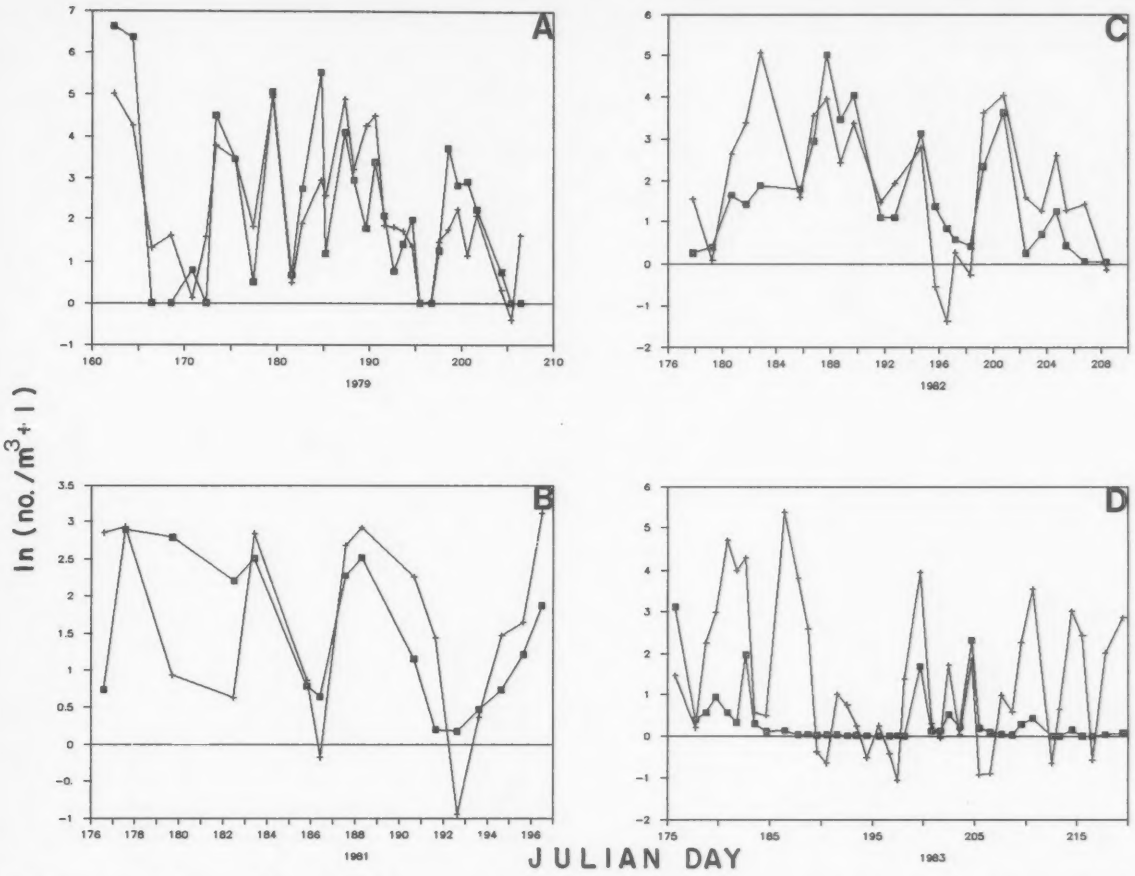


FIG. 2. Time series of observed (■) and modelled (+) variations in the inshore geometric average density of *Oikopleura* in Bryants Cove in (A) 1979, (B) 1981, (C) 1982, and (D) 1983.

TABLE 2. Parametric and nonparametric correlation coefficients for the observed and modelled *Oikopleura* density estimates. Sample size (n) and significance level (parentheses) are provided for each year.

Year	n	Pearson	Spearman
1979	32	0.786 (0.0001)	0.786 (0.01)
1981	16	0.555 (0.026)	0.605 (0.02)
1982	25	0.680 (0.0002)	0.744 (0.01)
1983	41	0.339 (0.030)	0.492 (0.01)

to calculate U_w at our location is universally applicable when it is generally understood that larger scale coastal upwelling is driven by longshore winds (e.g. Yao 1986). If the model is used for other locations the wind vectors *must* be resolved according to the downwind direction of winds that induce upwelling.

The model is currently restricted in application to the June–August period and has relatively poor predictive power in the first part of the season. This was particularly evident early in 1981 when the observed densities of *Oikopleura* were considerably higher than the modelled densities (Fig. 2B). During early summer the entire water column is cold (<5°C) and therefore ideal for *Oikopleura* to thrive, but their abundance is less predictable from the ambient wind condition. We expected that either water temperature or growing degree-days would account for this variation, but the data are sparse during the early June period and thus not adequately accounted for in the model.

Although the model reflected the oscillatory nature of the observed *Oikopleura* density in all years, amplitude was not well accounted for, particularly in 1983 (Fig. 2D). Failure of the model to account for extreme variations in amplitude is possibly due to the absence in the model of any biological variates such as phytoplankton production or standing crop (food for *Oikopleura*) and predator abundance and their interaction with *Oikopleura* population growth rates, fecundity, and generation time. These variables would obviously account for the intrinsic population dynamics of *Oikopleura* that are independent of water mass dynamics. However, our intent was not to model the population dynamics of *Oikopleura* absolutely, but simply to account for the relative abundance of *Oikopleura* (and therefore slub) in the inshore by examining the water mass dynamics. Although such biological variates may improve the model, they

TABLE 3. Temperature ranges (°C) coincident with high cod catch in various seasons and locations reported in the literature.

Temperature (°C)	Season	Location	Source
0–6	Feb.–May	Southern Grand Bank Div. 3-O, 3N	Thompson 1943
3–5	May–June	Spitzbergen	Lee 1952
3.5–4	Aug.–Nov.	(Bear Island)	
−1–4	Summer	Grand Bank Div. 3L	Rodriguez and Rojo 1955
0–5	Summer	Inshore Div. 2J, 3KL	Templeman and Fleming 1956
−1–4	May–June	Southern Gulf of St. Lawrence and Laurentian Channel	Martin 1961
0–6	Summer	Gulf of St. Lawrence	Jean 1964
1–8	Summer	Scotian Banks	
2.5–3.1	April–May	Hamilton Bank Div. 2J	Templeman and May 1965
−0.8–8.7	June		
−0.5–5	Summer	Barents Sea	Woodhead and Woodhead 1965
2–4	All	Scotian Shelf Div. 4Vn, 4Vs	Scott 1982
−0.9–4	June	Inshore and offshore Div. 3L	Lear et al. 1986

Median = 2.9

are generally unavailable and would effectively reduce the utility of the model to other workers if such variables were incorporated. Autecological studies of *Oikopleura* species have shown that the clearance rates of *O. vanhoeffeni* are high (< 15 L/d), and the species could have a major impact on phytoplankton populations (Diebel and Turner 1985), but how *Oikopleura* populations respond (if at all) to phytoplankton production and predation pressure is unknown.

One variable likely to provide the greatest improvement to the model is the generation time of the cold-water *Oikopleura* species, but it is unknown. Generation times have been measured for the warmer-water species *O. dioica* (preferred temperature range 7–18°C) and were estimated to fall between 24 and 144 d (Paffenhöfer 1975; Wyatt 1973). It is probable that the generation times for the cold-water species are greater than their warm-water congeners, and the limited data available indicate that there may ony be one or possibly two generations each year (D. Diebel, Mar. Sci. Res. Inst., Memorial University of Newfoundland, St. John's, Nfld., pers. comm.). If there are only one or two generations each year, then adding this information to a model that makes predictions on the scale of days would probably yield limited improvement.

We suggest that the relatively low predictive power of the model in 1983 may be the result of increased surface water temperature in 1983 that either limited the development of normally large populations of *Oikopleura* or limited their appearance inshore due to an increased depth of the surface layer which would require stronger than average and more persistent offshore winds to induce upwelling. It is widely recognized that 1983 was an anomalous year throughout the Northwest Atlantic with record high sea-surface temperatures (Trites and Drinkwater 1985). A summary of the water temperature data from our study (see below) is consistent with the suggestion that warm water temperatures limited the occurrence of *Oikopleura* in 1983 relative to the other years:

	Temperature (°C)					Average *Oikopleura* density
Year	Minimum	Maximum	Mean	CV	*n*	(no./m^3)
1979	0.4	11.1	5.05	51.7	47	8.78
1981	0.0	13.0	6.98	44.7	528	4.25
1982	1.48	11.55	6.96	28.4	1439	4.98
1983	−0.97	15.70	7.40	36.9	1295	1.44

It is important to note that in 1979 the average water temperature in Bryants Cove was the lowest among the four years and coincided with the greatest average abundance of *Oikopleura*. Also, intermediate temperatures in 1981 and 1982 corresponded with intermediate *Oikopleura* densities. However, while the surface temperatures were anomalously high in 1983, the subsurface temperatures were anomalously low (Lear et al. 1986). The minimum temperature measured in Bryants Cove in 1983 (above) is in agreement with the findings of Lear et al. (1986) and suggests the alternative possibility that *Oikopleura* production was limited in 1983 by colder than average subsurface temperatures.

Implications to the Inshore Fishery

The results of our analysis suggest that to avoid slub conditions and the fouling of nets in the inshore, fishermen could pursue several options: (1) avoid setting nets below the seasonal thermocline; (2) avoid locations where upwelling conditions and cold temperatures prevail; (3) retrieve nets from locations when upwelling favourable winds prevail at the location; or (4) clean nets after a period of upwelling favourable winds. However, with the exception of (4), such actions may reduce the catch.

Cod catches in the Northwest Atlantic and elsewhere are generally greatest at a median temperature of 2.9°C (range −1 to 8; Table 3) which overlaps the range associated with the high

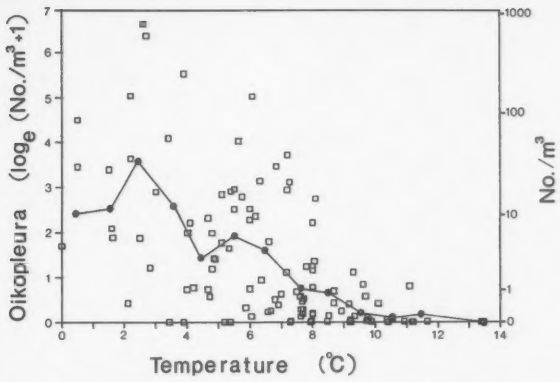


FIG. 3. Scattergram of the relationship between temperature and *Oikopleura* density for the years 1979 and 1981–83 combined in Bryants Cove. The average densities of *Oikopleura* for each 1° step in temperature are joined with a solid line.

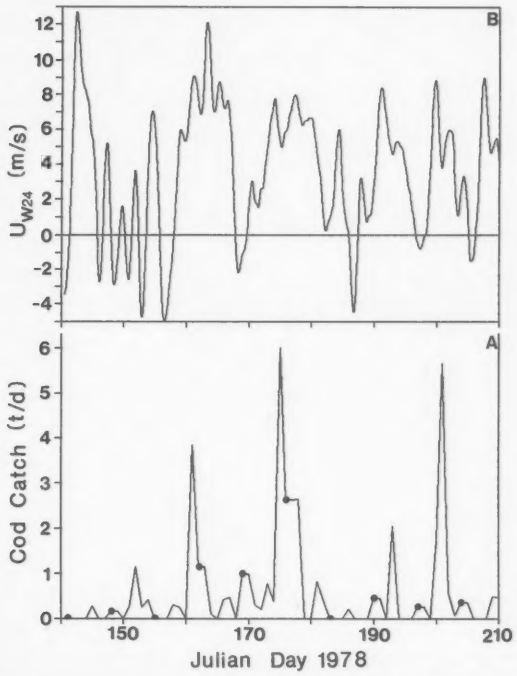


FIG. 4. Time series of (A) daily inshore cod catch and (B) U_{w24} in 1978 at Bryants Cove. No fish were landed on Sundays (●), and therefore, the catch recorded on Monday was divided equally between the two days.

densities of *Oikopleura* (Fig. 3). This observation provides support for the suggestion that cod and *Oikopleura* co-occur in the inshore, particularly under conditions of wind-driven upwelling. We qualitatively evaluated this suggestion by examining the relationship between the daily cod catch from an inshore trap in Bryants Cove in 1978 and U_{w24}. Cod catch (tonnes per trap per day) was taken from the 1978 landing records provided to us by Mr. W. Parsons (resident fisherman of Bryants Cove).

The largest catches of cod recorded in 1978 (Fig. 4A) were associated with the onset of prolonged periods of offshore (upwelling favourable) winds (Fig. 4B), although there are inconsistencies at the beginning and at the end of the series. Nevertheless, the pattern is very similar to those shown for the abundance of *Oikopleura* relative to offshore winds (Fig. 1). These results support the suggestion that wind conditions associated with high catches of cod are coincident with conditions favourable to high *Oikopleura* density and lend credence to reports that fishermen catch fish near fouled gear when using other gear such as jiggers or trawls (Diebel 1987).

Fishing nets are not fouled immediately at the onset of upwelling conditions because slub is a cumulative phenomenon, i.e. a function of the duration of upwelling and the local *Oikopleura* density. This led us to hypothesize that catch would be highest near the start of an upwelling period and lower near the end of the same period due to a decrease in trap efficiency caused by net fouling. The hypothesis cannot be adequately tested with the data available, but we point out that cod catch did not remain high during prolonged offshore winds (Fig. 4) as did the abundance of *Oikopleura* (Fig. 1). Alternatively, catch may be reduced during persistent upwelling because of continuously declining temperature. The data available are not suitable for the rejection of either hypothesis.

The apparent relationship between wind and cod catch (Fig. 4) is not new. Jeffers (1931) reported that "The opinion is well-nigh universal that winds are of particular importance in determining the movements of cod." Templeman (1966) suggested that cod catch in the inshore trap fishery was a function of temperature preference of cod, trap position with respect to depth, thermal structure of the water column, and wind condition. This view was echoed by Lear et al. (undated).[2] Simply restated, Templeman (1966) recommended that nets be set at a depth which intercepts the seasonal thermocline, the zone which spans the cod temperature preference. Buggeln (1978) suggested that traps are inefficient during slub conditions because the water is too cold for cod and not because of fouling. The evidence we have presented does not support Buggeln's suggestion in general, although during periods of persistent upwelling (say >2 d) the interpretation may be correct. Nevertheless, if fouled nets are used when ideal conditions for cod exist, it is very likely that catch will be relatively poor. This implies that to be most successful, fishermen must be wary of the water mass dynamics and fish at depths and locations that allow for a frequent interception of the seasonal thermocline, thus increasing the probability of greater catch and decreasing the probability of net fouling.

Our model could be used to generate an historical time series of slub conditions for each year (a computer program for calculating U_w and generating the slub time series is available on request from the authors). An index of the severity of slub for each year could be provided by the integration of the time series, similar to the integrated wind index described by Taggart and Leggett (1987). Tentative support for such an approach is found in a comparison of the "slub years" in Nova Scotia documented by Buggeln (1980) with the annual sea-surface temperature (SST) anomalies for the 1951–81 base period at St. Andrews and Boothbay Harbour (Trites and Drinkwater 1985). Of the six

[2]W. H. Lear, C. A. Bishop, and P. R. Hood. Undated. Trap cod. Some facts about unpredictable catches and small fish. Communications Division, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld. A1C 5X1. 16 p.

slub years considered, 1966, 1967, 1972, and 1980 had anomalously low SSTs at both geographic locations. Near average SSTs existed at both sites during 1970 and 1979. We further suggest that the index can be compared with the inshore catch statistics for both cod and salmon, and in this manner the relationship between slub and catch could be quantified relative to other factors (e.g. temperature, prey availability, stock size, effort, etc.).

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Modelling the Effects of Accelerated Development and Reduced Fecundity on the Population Dynamics of Aquatic Diptera

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Rempel, R. S., and J. C. H. Carter. 1987. Modelling the effects of accelerated development and reduced fecundity on the population dynamics of aquatic Diptera. Can. J. Fish. Aquat. Sci. 44: 1737–1742.

The population dynamics of aquatic insects were simulated using a stage-projection matrix model. Transition elements, some of which were specified by nonlinear and stochastic functions, represent the joint probability of development and survivorship from time t to $t+1$. For the simulation, stage-specific survivorship was kept unchanged and only development rate and fecundity were altered. The simulation predicts that the intrinsic capacity for population growth (r_m) and equilibrium levels of abundance (K) should increase with both faster development rate and higher fecundity, independent of stage-specific mortality. As a test of the effect of accelerated development on population growth, abundance of insects emerging from experimental stream channels was compared in ambient temperature and heated channels. Development was faster in the heated channels, and abundance was greater for 9 of the 11 species compared. These results indicate that changes in development rate, in addition to changes in fecundity, must be considered when predicting the population effects of an altered thermal regime.

On a effectué une stimulation de la démécologie d'insectes aquatiques à l'aidé d'un modèle par matrice de projection des stades de développement. Les éléments de transition, dont certains ont été déterminés à l'aide de fonctions non linéaires stochastiques, représentent la probabilité combinée du développement et de la survie du temps t au temps $t+1$. Aux fins de la simulation, la survie selon le stade de développement n'a pas été modifiée; seul le taux de développement et la fécondité l'ont été. La simulation prévoit que la capacité intrinsèque de croissance de la population (r_m) et les niveaux d'équilibre de l'abondance (K) devraient augmenter en fonction d'un taux plus élevé de développement et d'une plus grande fécondité, indépendamment de la mortalité selon le stade de développement. Pour vérifier l'incidence du développement accéléré sur la croissance de la population, on a comparé l'abondance des insectes émergeant de canaux expérimentaux à température ambiante et de canaux chaffés. Le développement a été plus rapide dans les canaux chauffés où 9 des 11 espèces comparées ont été plus abondantes. Les résultats indiquent que les variations du taux de développement doivent, en plus des variations de la fécondité, être examinées au cours des prévisions des incidences démographiques de régimes thermiques modifiés.

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The ecology of running water environments has been studied intensively over the last 25 yr (see Hynes 1970; Macan 1974; Barnes and Minshall 1983; Merritt and Cummins 1984; Resh and Rosenberg 1984), and many factors have been identified which play important roles in the dynamics of these systems. One such factor, temperature, has repeatedly been cited as an important controlling agent (e.g. Sprules 1947; Macan 1961; Hynes 1970; Sweeney 1984), yet our knowledge of the mechanism by which temperature affects the distribution and abundance of organisms is still rudimentary. Such knowledge is necessary to predict successfully the consequences of altering a thermal regime. Clear-cut logging, agricultural removal of riparian vegetation, release of thermal effluents from nuclear and coal-fired power plants, and discharge from hydro-dams can all alter the natural thermal regime of aquatic systems.

Some theories (Sweeney 1984) have been formulated to generalize the effect of temperature in streams based on responses of fecundity and body size. For example, Vannote and Sweeney (1980) "suggest that an 'optimum' thermal regime exists where adult size and fecundity are maximized." However, one parameter, development rate, has been left almost unconsidered in its effect on aquatic insect population dynamics, even though the theoretical importance of age at first reproduction has been recognized for quite some time (Cole 1954; Lewontin 1965). Given that mortality rates differ among stages, the rate instars pass through these stages towards maturity may have important implications on population parameters. In a companion paper, we investigated exerimentally the influence of temperature on adult size, development, and fecundity of aquatic Diptera (Rempel and Carter 1987).

In this paper, we simulate increased development rate and decreased fecundity to determine the effect these factors have on an aquatic insect's capacity for population growth (r_m) and

[1]Deceased.

equilibrium level of abundance (K). The results of the simulation are tested with emergence data of 11 insect species collected from outdoor experimental stream channels where a ΔT of 4°C was maintained between ambient and heated treatments. Most species examined were Diptera and can be considered opportunistic in that they are small, develop rapidly, and, depending on environmental conditions, can have one or more generations per year.

Methods

Model

The simulation model was derived from the stage-transition matrix model (Lefkovitch 1965), itself a generalization of age-transition model (Leslie 1945). The stage-transition model is especially appropriate for holometabolous groups like the aquatic Diptera because determining the age of a larva can be impossible, especially if extended egg deposition and hatching occurs. Developmental stages, however, are easily recognized.

In the Lefkovitch model, the expected number of individuals of stage j alive at time $t+1$ per living individual of stage i at time t is equal to

$$\Pr(j, t+1 \mid i, t, a)(\mathrm{Em}(j \mid i; t, t+1))$$

where a indicates that the individual is alive, Pr() is the probability of being alive in stage j at $t+1$ given that it was alive in stage i at time t, and Em() is the expected number of individuals of stage j which result from an individual of stage i for the interval $(t, t+1)$.

In the model presented here, the first term of the above expression is decomposed as

$$m_{j,i} = \Pr(j, t+1 \mid i, t)\Pr(a, t+1 \mid i, a, t)$$

where $m_{j,i}$ is an element of the transition matrix. This extends the generality of the stage-transition model by separating the probability of transition ($m_{j,i}$) into two component parts, the probability of development from stage i to j, and the probability of survivorship, over the time interval $t, t+1$, i.e. the joint probability of development (D) and survivorship (S). Note that in invertebrates such as large decapods where transformation from stage i to j may be hazardous, the independence of D and S cannot be assumed. For aquatic Diptera, molts are of very short duration, and this added complexity was not estimated in the model.

If the transition probabilities vary with time, then the population is best modelled by a series of transition matrices. For example, consider the equations in a system that has four seasons, with a matrix of transition elements representing each season:

$$\boldsymbol{M}_1\boldsymbol{x}_0 = \boldsymbol{x}_1,\ \boldsymbol{M}_2\boldsymbol{x}_1 = \boldsymbol{x}_2,\ \boldsymbol{M}_3\boldsymbol{x}_2 = \boldsymbol{x}_3,\ \boldsymbol{M}_4\boldsymbol{x}_3 = \boldsymbol{x}_4$$

The series can be expressed as a product of transition matrices, such that

$$\boldsymbol{M}_1\boldsymbol{x}_0 = \boldsymbol{x}_1,\ \boldsymbol{M}_2\boldsymbol{M}_1\boldsymbol{x}_0 = \boldsymbol{x}_2,\ \boldsymbol{M}_3\boldsymbol{M}_2\boldsymbol{M}_1\boldsymbol{x}_0 = \boldsymbol{x}_3,$$
$$\boldsymbol{M}_4\boldsymbol{M}_3\boldsymbol{M}_2\boldsymbol{M}_1\boldsymbol{x}_0 = \boldsymbol{x}_4.$$

Conceptually, the series of matrices $\boldsymbol{M}_4\boldsymbol{M}_3\boldsymbol{M}_2\boldsymbol{M}_1$ can be viewed as the produce $\boldsymbol{M}$, so that

$$\boldsymbol{M}\boldsymbol{x}_0 = \boldsymbol{x}_4.$$

If elements of a matrix are best modelled by a nonlinear function, such as might arise when density-dependent competition or predation occurs, or if elements are best considered stochastic, as might arise when density-independent mortality caused by physical conditions is substantial, then it is possible to calculate these elements separately and substitute them into the appropriate matrix prior to multiplication at each iteration. For example, consider a stage i whose probability of survivorship from time t to $t+1$ is dependent on the density of stage i at time t. Then $s_i = f(x_k)$ where f is some nonlinear function specifying the effect of abundance on survivorship. At each iteration during simulation, these elements are calculated from suitable functions and the current expected number of individuals within the appropriate stage.

These extensions in the stage-transition matrix model greatly increase the realism and application of the model, freeing it from restrictive assumptions concerning stable age distributions within stages, the invariance of stage-specific mortality and development, and the linear response of population growth to density. However, certain analytical properties, such as the dominant latent root (eigenvalue) of the transition matrix (λ), cannot be obtained directly. This root is of interest because its natural logarithm is equivalent to the instantaneous rate of increase, i.e.

$$\ln(\lambda) = r.$$

In the simulation model, intrinsic rates of population growth (r_m) and equilibrium levels of abundance (K) are obtained from statistical analysis of the simulation results.

The simulation model was programmed in Modula-2, a Pascal-type language, on the Apple Macintosh computer (128k). To save memory space, nonzero elements of the sparse matrices were stored in a record data structure and only assigned to the matrix just prior to multiplication at each iteration. The model utilized eight square matrices, of order 7, and some of the elements were computed from either stochastic or nonlinear functions. Solution of the stochastic and nonlinear functions were also conducted just prior to multiplication.

Elements

The estimates of survivorship (Table 1) for the generalized aquatic insect were based in large part on a detailed study of *Chironomus anthracinus* in Lake Esrom (Jónasson 1972). Example calculations of D and S are provided in appendix A *in* Rempel (1987). Probability of survivorship essentially follows the Pearl type III survivorship curve (Krebs 1978), with the exception that loss of eggs through predation and physical damage, and hatching success of the eggs is included as a survivorship component. Also, unlike the Pearl model, survivorship during emergence decreases from the previous stages in aquatic environments due to heavy fish predation.

Density-dependent effects are simulated by the function

$$S = 1 - 0.7e^{(\mathrm{adults}\cdot 0.0000059)}$$

where S is the survivorship of instar 1 and adults is the final population size of the previous generation. Jónasson (1972) provided convincing evidence that density-dependent predation affected survivorship of egg and 1st instar stages; in our general aquatic insect model, survivorship of 1st instar larvae was defined as the density-dependent stage. High densities of egg clusters, for example, serve as easy prey for predators, as would 1st instars that have not found suitable safe habitat. Similarly, the probability of surviving spring and fall floods or summer drought is density dependent if suitable habitats are limited in number (Smith 1935).

TABLE 1. Nonzero elements of transition matrices for the initial development rate. D = "i" and "a" for initial and accelerated development rates, respectively.

Matrix	Stage[a] j (column)	Stage i (row)	Probability of development (D)		Probability of survivorship (S)
			i	a	
1 (May)[b]	7	1	1	1	3000 (2550)
2 (June)[c]	1	1	1	1	0.25
3 (July)[d]	1	2	0.8	0.8	0.05
4 (Aug.)[e]	2	2	0.4	0.1	$S(f_1)$
	2	3	0.3	0.5	$S(f_1)$
	2	4	0.3	0.4	$S(f_1)$
5 (Sept.)[f]	2	4	1	1	$S(f_1)$
	3	3	0.6	0.4	0.9
	3	4	0.4	0.6	0.9
	4	4	0.98	0.7	0.9
	4	5	0.02	0.3	0.9
6 (Oct.)[g]	3	4	0.67	0.5	0.9
	3	5	0.33	0.5	0.9
	4	4	0.18	0.05	0.9
	4	5	0.82	0.95	0.9
7 (Apr.)[h]	4	6	1	1	0.59
	5	6	1	1	0.59
8 (May)[i]	6	7	1	1	0.57

[a]Stage 1 = egg, stages 2–5 = instars 1–4, stage 6 = pupae, stage 7 = adult.
[b]S represents fecundity (number of eggs per individual) for initial (and reduced) fecundity states.
[c]S represents losses from physical damage during prehatch period.
[d]D represents hatching success.
[e]Survivorship of stages is dependent on population density. i.e., $S\ (f_1) = 1-0.7e^{(\text{adults}\cdot 0.0000059)}$.
[f]Survivorship of stages 3 and 4 in September is modelled by a random binomial deviate, with 1–0.9 as the parameter (p) for the binomial expression.
[g]Survivorship in October is nonrandom.
[h]Survivorship rate over 5 mo is cumulative, i.e. $e^{(\ln 0.9\cdot 5)}$.
[i]Decreased survivorship during pupation and emergence.

The form of the equation used to simulate these effects is similar to the one used by R. Law to describe density dependence in *Pao annua* seedlings (cited in Begon and Mortimer 1981). Adults, rather than the number of eggs produced by the adults, was used in the equation to avoid programming floating-point computations with very large numbers. Probability of survivorship ranges from 0.3 when number of adults is 0 to approximately 0.203 at equilibrium levels of abundance (approximately 22×10^3 adults). Although the function S can theoretically be negative if the number of adults is very large, at high levels of population abundance (e.g. 60×10^3 adults), survivorship would drop to 0.003 of instar 1 larvae, effectively preventing S from ever becoming negative.

The stochastic functions simulate the cumulative effect of various density-independent factors and were used to calculate survivorship of 2nd and 3rd instars in matrix 5 (September). Because survivorship is essentially a Bernoulli event in that an animal can either live or die over a given period, it was simulated by the binomial function

$$S = 1 - k/N$$

where S is survivorship, k is the number of successes, and N is the number of trials. Successes refers to the frequency of the N uniform random numbers greater than or equal to the specified binomial parameter p. The survivorship density function will have a single mode of approximately $1 - p$. For the simulation, 32 trials (N) were used to generate each binomial deviate.

There are probably other specific functions not included here which further research in aquatic ecology might reveal to be important. However, only functions for which clear effects in aquatic systems have been established were included. For example, in terrestrial insects, fecundity has been shown to be density dependent (e.g. Watt 1960), although for aquatic insects little is known about these effects. In contrast with other systems, larval populations in running waters can easily disperse in situations of low food resource levels by drifting downstream, potentially mitigating the effects of high densities on individual growth and fecundity (Hawkins 1986). Hence, density effects on fecundity were not modelled.

Simulation Experiment

A 2^2 factorial experiment was conducted with the following states of development and fecundity: (1) initial fecundity = 3000 eggs per individual; (2) reduced fecundity = 2550 eggs per individual; (3) initial development rate; (4) accelerated development rate. Note that for each matrix, the probability of developing for each stage sums to 1 (Table 1). Estimates of initial development rates were derived in large part from Jónasson (1972). Accelerated development only affects matri-

ces 4, 5, and 6 where probabilities of development to a succeeding stage are less than 1 (hatching success in matrix 3 was not altered). Fecundity was diminished by 15% for the reduced fecundity state. The decision to lower fecundity by this amount was based in part on results from the experimental study at Perch Creek (Rempel and Carter 1987). Results from the study indicated that although development rate increased, and body size decreased for most species, ovary size remained constant, or at least decreased at a much lower rate than did body size. The average decrease in female body size in 1984 was 31.5%, and a reduction in ovary size of about one half this figure is consistent with the Perch Creek data.

Each simulation ran for 30 generations, and each state was replicated 10 times. Intrinsic rates of increase (r_m) were calculated as the slopes of ln(total adults) versus generation number for the first five generations. During the first five to eight generations, density-dependent effects have not occurred, and the population is increasing geometrically. Equilibrium levels of abundance (K) were calculated from ln(adults) of generations 20–30. Analysis of variance was conducted on these two response variables. Homogeneity of variance of the r_m values was tested by conducting a one-way ANOVA on the deviations of cells means (Levene 1960). In this paper, K is broadly defined as the equilibrium level of abundance for any population model, not strictly the equilibrium parameter for the logistic model (Lotka 1925).

Field Experiment

The simulation experiment produced an hypothesis concerning the regulation of population growth in stream insects, and this was tested with field experimental data presented in part in the companion paper (Rempel and Carter 1987). The simulation experiment was conducted before any statistical analysis of the hypothesis was carried out. The field experiment consisted of elevating the temperature in four outdoor stream channels; a ΔT of 4°C between two ambient and two heated channels was maintained in 1984. Emergence traps were used to estimate abundance, and data were ln transformed prior to analysis because variances are typically positively correlated with means for aquatic invertebrate abundance data (Elliott 1977). Part way into the experiment, one heated channel was rendered unusable, and as a consequence we placed two traps on the remaining heated channel (separated by approximately 3 m) and treated them as distinct samples. This somewhat weakens the external validity of the statistical analysis, but because the hypothesis resulting from the simulation was defined a priori, the statistical test of it is still valid.

Results and Discussion

Increasing the development rate from the initial state resulted in a significantly greater intrinsic capacity for population growth (r_m) (Fig. 1; Tables 2 and 3). In addition, K, the equilibrium level of population abundance, also increased. These responses occurred independently of stage-specific survivorship, as survivorship parameters were left unaltered throughout the simulation experiment. Survivorship was lowest in the early stages and increased as the cohort developed (Fig. 2). Differences in development rate between initial and accelerated states occurred only at $t = 4$–6 (corresponding to matrices 4–6). Mean stage is not shown for the accelerated development state, but was approximately 12% greater at $t = 4$ and 4% greater at $t = 5$ and 6 after faster development. Because instar duration is shorter in the earlier stages, the greater response at $t = 4$ is probably realistic.

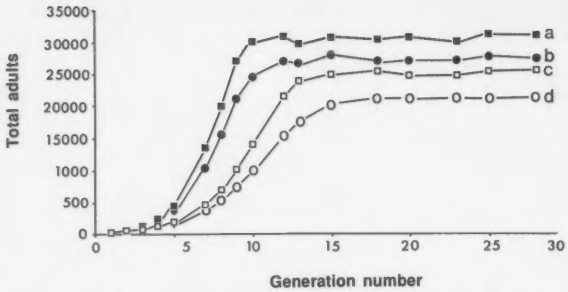

FIG. 1. Simulated population growth over 30 generations. Solid symbols refer to initial fecundity, open symbols to reduced fecundity, round symbols refer to initial development, and square symbols to accelerated development. Each symbol represents the mean of 10 simulations, and standard errors of the mean in all cases fall within symbol area. Letters refer to means in Table 3.

TABLE 2. ANOVA statistics from simulation experiment (two-way, fixed effect; there were two levels for both development and fecundity).

Source	df	MS	Probability no effect
r_m values[a]			
Development	1	0.0130	<0.0001
Fecundity	1	0.2573	<0.0001
Interaction	1	<0.0001	0.978
Error	36	0.0002	
K values			
Development	1	0.1983	<0.0001
Fecundity	1	0.4956	<0.0001
Interaction	1	0.0048	<0.0001
Error	36	0.0003	

[a]Variances of r_m values were homogeneous ($p = 0.598$).

TABLE 3. Mean r_m and K values (with SD) for two levels of fecundity and development.

Fecundity[a]	Development	r_m	K[b]
Initial (*a*)	Accelerated	0.6144 (0.0168)	10.329 (0.0147)
Initial (*b*)	Initial	0.5781 (0.0156)	10.210 (0.0104)
Reduced (*c*)	Accelerated	0.4537 (0.0128)	10.128 (0.0236)
Reduced (*d*)	Initial	0.4180 (0.1280)	9.9660 (0.0140)

[a]Letters refer to lines in Fig. 1.
[b]K values are means of ln (total adults) of generations 20–30.

Reducing fecundity by 15% resulted in a decrease in both r_m and K. The response of K to fecundity, however, was not equal at different development rates. The interaction between development and fecundity was significant (Table 2), with a slightly lower response of K to fecundity at accelerated development rates (Table 3). Within the boundaries of this experiment, development rate has proportionally more influence on abundance than fecundity.

Results of the simulation experiment suggest that insect abundance should respond immediately to elevated tempera-

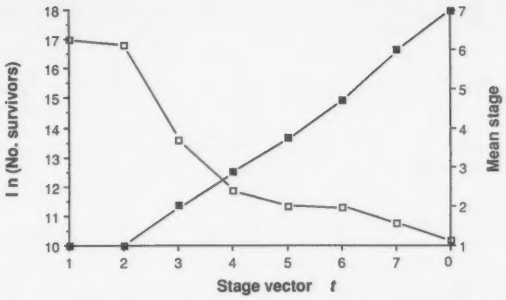

FIG. 2. Simulated population survivorship and development over the eight sampling periods (= iterations). Solid symbols refer to surviving population, irrespective of developmental stage, and open symbols refer to mean instar stage. Each symbol represents the mean of 10 simulations (generations 25–30 for two runs), and standard errors of the mean for total population size in all cases fall within symbol area.

ture, irrespective of any long-term changes in fecundity, if development rate is increased. This response would be based solely on enhancement of the intrinsic capacity for population growth. Rempel and Carter (1987) have shown that for virtually all insects emerging from the experimental channels during summer, development was faster at the elevated temperature. To test the hypothesis, we compared total emergence from the experimental channels for 11 species. Abundance was significantly higher in the heated channel (Table 4), and 9 of the 11 species increased in abundance in the heated channel (Table 5). Only *Polypedilum aviceps* and *Parametriocnemus lundbecki* decreased in the heated channel. Most of the insects were polyvoltine; however, the number of generations for each species (emergence phases) was constant for both temperatures, and emerging insects were unrestricted in their flight away from the channels. Thus, neither changes in number of generations nor fecundity of adults ovipositing for second and subsequent generations can account for the increases in abundance.

Although the results of the simulation are straightforward, and probably not too unexpected, they have important implications in traditional concepts of how temperature affects community structure of stream ecosystems. For example, Vannote and Sweeney (1980) hypothesized that the geographic distribution of some aquatic insects may be limited by lowered fecundity in nonoptimal thermal regimes, and they stated that decreased body size is indicative of nonoptimal conditions. However, decreased body size does not necessarily result in an equal drop in fecundity in holometabolous insects (Rempel and Carter 1987), and the results from this simulation suggest that accelerated development can significantly increase both the colonizing potential of the species (r_m) and its equilibrium level of abundance (K)

The cause of the effects on r_m with respect to development time requires some explanation. Theorists have shown that for colonizing populations, decreasing the age at first reproduction (A) results in an increase in r_m (Cole 1954; Lewontin 1965) and that A has relatively greater effect on r_m than fecundity. For example, Lewontin (1965) found that in terms of its effect on r, decreasing A from 8.6 to 7.5 d for two races of *Drosophila serrata* was equivalent to doubling the total number of progeny produced. In these stable age distribution models, r_m is calculated from the expected number of offspring (V_x), (i.e. the product of age-specific survival (l_x) and birth rates (m_x). Considering only accelerated development, in our stage-

TABLE 4. ANOVA (fixed effect) for emergence data from experimental channels at Perch Creek. Mean emergence is interpreted as mean abundance·0.3 m^{-2}.

Source	df	MS	Probability no effect
Species	10	11.024	<0.0001
Temperature	1	5.098	0.0005
Interaction	10	1.038	0.0079
Error	22	0.305	

TABLE 5. Mean emergence·0.3 m^{-2} (with SD) of Diptera in ambient temperature and heated channels.

Species	Ambient	Heated
Chironomidae		
Ablabesmyia mallochi	10.0 (8.5)	41.5 (36.1)
Conchapelopia aleta	129.0 (4.2)	255.0 (86.3)
Corynoneura cf. *taris*	171.5 (27.6)	294.5 (87.0)
Nilotanypus fimbriatus	85.5 (34.6)	92.0 (31.1)
Parametriocnemus lundbecki	388.5 (258.1)	252.0 (128.7)
Polypedilum aviceps	305.0 (79.2)	155 (136.5)
Rheotanytarsus sp[a]	57.5 (2.1)	118.5 (82.7)
Stempellinella brevis	1991.0 (702.9)	4546.0 (1463.7)
Simuliidae		
Cnephia sp.	0.5 (0.7)	23 (12.7)
Simulium latipes	53.0 (14.1)	105.5 (79.9)
Similium venustum	157.5 (61.5)	467.0 (175.4)

[a]*Rheotanytarsus* sp. A in Rempel and Harrison (1987).

projection model, neither stage-specific mortality nor adult fecundity was altered, yet r_m increased. However, within a stage, the effects of instantaneous stage-specific mortality are cumulative with time, so decreasing time spent within a stage increases survivorship. In addition, the rates of survivorship are lower for the earlier stages. The higher r_m values, then, are explained by a greater expected number of offspring due to increased overall survivorship resulting from accelerated development.

The effect of A on equilibrium level of abundance (K) has not received the same theoretical attention. In Lotka's (1925) model, K is a parameter of the logistic equation defining the asymptotic density and is considered to be an independent parameter defined by characteristics of the environment. Results of the simulation suggest that K is not independent of A, rather it is highly dependent. Increasing overall survivorship is the probable cause for the higher population level at which this balancing occurs. This effect will likely differ depending on the type of survivorship schedule the organism has.

Population equilibrium occurs when birth rate matches death rate (i.e. $r = 0$) and the matrix product $M_8M_7 \ldots M_1$ presumably has within it a dominant latent root (λ) approaching unity. At the equilibrium condition, matrix elements are probably relatively constant, which suggest that the same result might have been obtained deterministically if these final elements had been used to define a matrix M. Hence, solution of a characteristic equation and subsequent matrix analysis is not necessarily precluded by adopting a simulation approach.

The lack of oscillatory behaviour in the equilibrium phase suggests that the model may be unrealistic with respect to population stability. Lefkovitch (1966) showed that when

fecundity is dependent on population density while larval females are developing, then periodic oscillations in abundance would occur. In such cases a higher order model, where the expected numbers at time $t + 1$ are dependent on the success of populations at times, t, $t - 1$, etc., may be more appropriate. However, as mentioned earlier, little evidence exists that density affects fecundity in aquatic insects or that populations in the relatively open stream ecosystems oscillate to the same degree as agricultural or forest pests. Where density is known to affect growth and development, this potential response should probably be considered carefully. The importance of fundamental life history parameters on K appears to be a relatively unexplored concept, and simulation techniques may provide the best means for theoretical analysis because of the complexities of the interactions. However, analytical investigations of matrix elements and the magnitude and complexity of latent roots may also provide additional insight.

Both these theoretical considerations and the experimental field results support the hypothesis that accelerated development should increase population abundance. The experiment lasted only one generation, so it is not known whether the higher levels of abundance observed are transitional or represent new equilibrium levels of abundance. Nonetheless, an important consequence of these results is that decreased body size, which often occurs due to faster development in elevated temperature, does not necessarily mean either the intrinsic capacity for population growth or equilibrium level of abundance is reduced. Both these population parameters might remain relatively unchanged, or actually increase with elevated temperature, even though body size decreases. The bioenergetic interpretation of fitness must, therefore, be considered carefully. Optimum somatic tissue production is not necessarily associated with optimum capacity to either survive or to produce gametes. Higher population survivorship at elevated temperatures can offset the negative effects of lower adult body size and provide resistance to thermal-induced perturbation. In contrast, reduced temperatures, with longer growth periods and lower metabolic rates, may result in larger adults at the expense of greater risk of mortality. These factors must be taken into consideration when predicting population response to altered thermal regimes. Hence, a thermal regime cannot be considered "suboptimal" simply because insects emerge smaller.

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Temperature Influences on Adult Size, Development, and Reproductive Potential of Aquatic Diptera

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Rempel, R. S., and J. C. H. Carter. 1987. Temperature influences on adult size, development and reproductive potential of aquatic Diptera. Can. J. Fish. Aquat. Sci. 44: 1743–1752.

Elevated temperature (2.5 and 4.0°C) resulted in smaller body size of stream Diptera in outdoor experimental channels, and this trend applied to both predator and detritivore trophic groups. Comparison of cumulative emergence curves using the Kolmogorov–Smirnov test showed that most species developed more quickly in the heated channels; this led to greater overall survivorship. Reproductive potential, estimated from ovary area, did not change with body size for *Conchapelopia aleta*, *Polypedilum aviceps*, and *Stempellinella brevis*, and did so only weakly for *Parametriocnemus lundbecki*. In addition, females decreased in size more than males in the heated channels. Somatic growth appeared to be sacrificed to maintain reproductive potential, although loss of energy reserves could reduce the length of the reproductive stage. In balance, the aquatic Diptera demonstrated resistance to thermal elevation in the summer, even though ambient temperatures approached 30°C. This may partially account for the group's ability to grow and develop throughout the year in extremely varied temperate environments.

Chez des diptères fluviaux gardés en canaux extérieurs expérimentaux, une plus petite taille corporelle a été le résultat de températures élevés (2,5 et 4,0°C); cette tendance a été notée chez les groupes trophiques de prédateurs et de détritivores. Une comparaison des courbes d'émergence cumulatives, à l'aide du test Kolmogorov–Smirnov a révélé que la plupart des espèces se développaient plus rapidement dans les canaux chauffés et présentaient donc une plus grande survie globale. Le potentiel reproducteur, tel que déterminé par la superficie des ovaires, n'a pas varié avec la taille corporelle chez *Conchapelopia aleta*, *Polypedilum aviceps* et *Stempellinella brevis* et n'a varié que légèrement chez *Parametriocnemus lundbecki*. De plus, les femelles ont accusé une plus forte réduction de la taille que les mâles gardés dans les canaux chauffés. La croissance somatique semble avoir été sacrifiée aux dépens du potentiel reproducteur quoique la perte des réserves énergétiques peut avoir réduit la durée du stade reproducteur. En contrepartie, les diptères aquatiques se sont montrés résistants à l'augmentation de la température en été, et ce, même lorsque la température ambiante s'est approchée de 30°C. Ceci peut expliquer en partie la capacité de croissance et de développement de ces groupes pendant toute l'année dans des environnements tempérés très variés.

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In stream ecosystems, it has long been realized that temperature plays an important role in determining the distribution and abundance of aquatic insects (Sprules 1947; Macan 1961; Hynes 1970; Vannote and Sweeney 1980; Ward and Stanford 1982). Although thermal lethal limits have been established for a number of aquatic insects (e.g. deKozlowski and Bunting 1981), the importance of temperature within those limits lies with the sublethal effects of temperature on life history parameters (Krebs 1978; Butler 1984). Most research has been conducted on hemimetabolus insects (Sweeney 1984); considerably less is known of the influence of temperature on holometabolous groups like the stream Chironomidae. As well, there are few studies comparing the response of different trophic groups to elevated temperature.

In a companion paper (Rempel and Carter 1987), we showed theoretically how two life history parameters, developmental speed and fecundity, can strongly influence the intrinsic capacity for increase and the equilibrium level of population abundance of aquatic Diptera. Both these life history parameters can potentially be altered by elevating temperature, and the purpose of our study here was to examine how an increase in summer temperature in a forested stream affects adult body size, rate of development, and reproductive potential of aquatic Diptera. Seven species (predominantly Chironomidae) from both the detritivore and predator trophic groups were included in the study.

The intent was to simulate a stream environment in the field using experimental channels, maintaining as many variables in their natural state as possible, and with a natural assemblage of organisms as similar to the originating stream as possible. The daily periodicity in temperature that occurs naturally in these midorder streams was left untouched; only one thermal variable, absolute temperature, was altered. Thermal variability has often been cited as an important physical parameter in running

[1]Deceased.

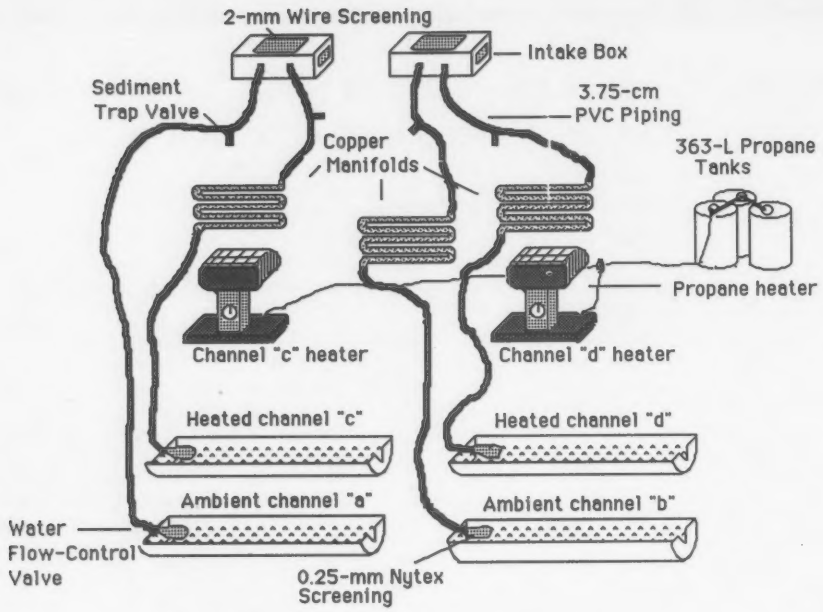


FIG. 1. Schematic drawing of the experimental stream system.

waters (Edington 1966; Sweeney 1978; Beck 1983), and we did not wish to increase the complexity of the experiment by altering this parameter in addition to absolute temperature. The realism of an in situ experimental study, however, can potentially cause ambiguity. The observed effects are net effects resulting from a myriad of interacting biotic and abiotic factors, including temperature effects on food resources. In a study reported on elsewhere (Rempel and Carter 1986), we independently examined how temperature affected food quality and quantity; this allowed us to assess the relative importance of temperature and food to the observed life history parameters.

Methods

Experimental Stream Channels

The experimental stream system was described in detail in Rempel and Carter (1986). Briefly, the system was constructed at Perch Creek, a heavily shaded stream located at the Chalk River Nuclear Laboratory (CRNL) research site, just north of Algonquin Park, Ontario (46°02′N, 77°22′W). The stream system consisted of four 6-m channels made from 30-cm-diameter PVC pipes cut lengthways (Fig. 1). The channels were placed on braces in a riffle section of Perch Creek, and during the first few weeks of the study (late April and early May of both years), water overflowed the channels. When water levels receded, the ends of the channels were blocked, and water to the channels was supplied by simple gravity feed through plastic drainage lines with intakes originating at an upstream waterfall. The water passed through a 0.25-mm nytex bag before entering the channels. The purpose of the filtering was to eliminate drift of all but the smallest organisms into the channel, but still allow fine particulate organic matter to enter. This ensured that organisms emerging from the channel indeed developed at the specified thermal regime and did not drift into the channel just prior to emergence.

The water heaters consisted of fourteen 0.5-m lengths of copper tubing, soldered together and placed above the burners of the two propane heating units. The flow-through system was designed to allow for a constant temperature differential (ΔT) between the ambient temperature and heated channels without dampening the normal pattern of diel periodicity in the thermal regime. Temperature was monitored in the middle of each channel using a continuously recording 90-d Ryan thermorecorder. Cumulative degree-hours per day were calculated as the cumulative sum of 12 temperature readings × 2. Two-hour intervals were chosen because they were easily obtained from the continuous thermal-record tape. Because the experiment was conducted during spring, summer, and early fall when temperatures were generally above 10°C (Rempel and Carter 1986), it was assumed that temperatures were almost always above the developmental threshold for the study species. In the text and on graphs, thousands of degree-hours are expressed as kilodegree-hours.

Emerging adults were collected with traps tightly fixed to the surface of the channels. Two types of trap were used on each channel. One was a live trap (1.35 m in length) designed to allow aspiration of newly emerged insects; these insects were used only for dissection of ovaries. Collections were generally made every weekday morning. The other was a modified LeSage–Harrison model WEEK emergence trap (1 m in length) that captured insects in a 10:1 alcohol–ethylene glycol preservative; these insects were used for determination of body size, emergence curves, and abundance. Unlike the model WEEK trap, our trap did not have a Plexiglas head, and insects flew directly into the collector jar (see fig. 4 *in* LeSage and Harrison 1979). This eliminated the problems associated with condensation on the heads. The traps were emptied about every 3 d. Sticky insect tar was used to seal possible openings, and "curtains," made from nylon insect screening, were placed at the upstream and downstream edges of the traps to prevent adults entering from outside the channels.

For this paper, the two ambient channels were labelled "a" and "b" and the heated channels "c" and "d." In 1983, the ΔT between channels was originally set at 4°C, but when ambient stream temperatures approached 30°C (June 12) the ΔT was reduced to 2.5°C for the remainder of the year. A 4°C ΔT was maintained throughout the study in 1984. Midway through the 1984 experiment, heated channel "d" was accidentally pulsed with a lethal dose of hot water – as a consequence, only three channels, ambient "a" and "b" and heated "c," were used for the rest of the experiment. In 1984, water flowed through the copper piping before entering the channel for ambient channel "b," but not for channel "a" (Fig. 1). This was done to provide some evaluation of the effect copper might have on the fauna.

Estimation of Life History Parameters

Adult emergence was used to evaluate the effect of elevated temperature on overall developmental rate. Late-instar larval colonization occurred synchronously in the heated and ambient channels in early spring, and egg deposition and early-instar colonization occurred synchronously in late spring/early summer. For each treatment, the emergence data were cast as a relative cumulative frequency distribution. The Kolmogorov–Smirnov two-sample goodness-of-fit test was then used to test whether the relative cumulative distributions differed (Siegel 1956). Differences in distributions will occur if either the timing or dispersion of the emergence phenology differs, so some caution is required in interpretation of significantly different distributions. (A more disperse emergence trend is distinguished by a less acute slope.) If the emergence occured in two easily separable phases, a relative cumulative distribution was cast for each phase. Max D, the maximum vertical distance between curves, is the test statistic.

The difference in dates at which 50% of the insects emerged (i.e. the horizontal distance between curves at 0.5 relative cumulative emergence) provides a general indication of advancement in overall emergence. Statistics were not applied to these values. Again, some caution is required in interpreting these values if inflection in the emergence curve happens to occur at about the 0.5 mark.

Measurements of wing and abdomen length were made to estimate body size. Wing length has a biophysical link with body size, as wing surface area would be expected to increase with body weight to maintain flight capability. The abdomen comprises the major portion of the body weight and is thus highly linked with overall body size. There was some concern that the proportion of body parts might differ if development rate was altered, so analysis of covariance was used to estimate if wing length and abdomen length remained in the same proportion in the heated and ambient channels, i.e. if the slopes describing the relationship between wing length and abdomen length differed between temperature treatments. Except for two groups, male *Polypedilum aviceps* (1984) and male *Microtendipes pedellus* (1983), all species had homogeneous regression lines between treatments ($p = 0.01$). Thus, for most of the 20 groups compared, proportional growth responses were the same between treatments, and either abdomen or wing length could provide a valid measure of body size. (Because of the large number of comparisons made, a type 1 error level of 0.01 was chosen; *P. lundbecki* females (1983) had p values of 0.035, which was considered nonsignificant.)

Both wing length and abdomen length are thus valid estimates of body size, but because wing length can be measured more accurately than abdomen length, wing length was chosen as the superior estimate of body size. There is less danger of changes due to preservation, and arculus and wing tip have very clear boundaries. Although wing length was linearly related tc abdomen length, there is strong theoretical reasoning (Gunther 1975; Peters 1983) and empirical evidence (Svensson 1975; Rogers et al. 1976, 1977; Smock 1980) that any appendage or abdomen length will be allometrically related to overall body size. Therefore, the natural logarithm (ln) of wing length was used as the best estimate of body size.

Ovary size was used as an estimate of reproductive potential i.e. the potential ability to produce viable gametes. Dipteran ovaries were compact and oval, and egg development occurred largely before emergence. A valid index of reproductive potential was difficult to derive, partly because eggs were tightly bundled in an ovarian egg mass which made counting their number impossible. As a first estimate of ovary size, the cross-sectional area of the ovary was determined. The ovaries were dissected from fresh, unpreserved adults. Ovary outlines were drawn on paper using a drawing mirror and then cut and weighed (gravimetrically integrated). In some species of Diptera the follicles continue to increase in size somewhat after emergence. Thus the size of the ovary may be related to the physiological age of the adult, in addition to adult body size. This increase in size occurs through the deposition of yolk and vitellin into the follicle. Hence an ovary's size will be partly a function of egg size, which is in turn a function of the physiological age of the ovary. Scattergrams showed that ovary size was in fact highly related to egg size for most species, so egg area (ln (egg length × width)) was included in the multiple regression model relating body size to ovary size. The ln egg area was not significantly related to ln wing length for any species ($p = 0.05$), so egg size was considered primarily a function of its physiological age after emergence.

Results

Experimental Channels

The flow-through heating system caused an increase in absolute temperature and cumulative degree-hours (Fig. 2), but did not dampen the normal diel periodicity in temperature (Fig. 3). Seasonal periodicity in temperature was also unaffected (Rempel and Carter 1986). Temperature in the "ambient" channels did not differ more than 0.5° from natural stream temperatures. Temperatures in Perch Creek range from a high of about 28–30°C in summer to 0.1°C in winter, and the high summer temperatures probably result from the stream flowing through an open marsh, about 1 km upstream. The alternation between open and forested habitat is typical of Shield streams, as are the high summer temperatures (Rempel and Harrison 1987).

Copper increased slightly from 15 $\mu g \cdot L^{-1}$ in the ambient channel "a" to 18 $\mu g \cdot L^{-1}$ in ambient channel "b" and 25 $\mu g \cdot L^{-1}$ in heated channel "c" in 1984 (Rempel and Carter 1986). Research on the influence of humic substances on copper toxicity indicates that the high particulate and colloidal levels in this brownwater stream would probably mitigate any toxicity of the copper (Winner 1984). Autotrophic organic layers, which are generally first affected by copper toxicity, actually increased in the heated channels, where copper levels were higher (Rempel and Carter 1986).

Invertebrate colonization of the channels occurred through the initial addition of loose substrate and rock packs, through

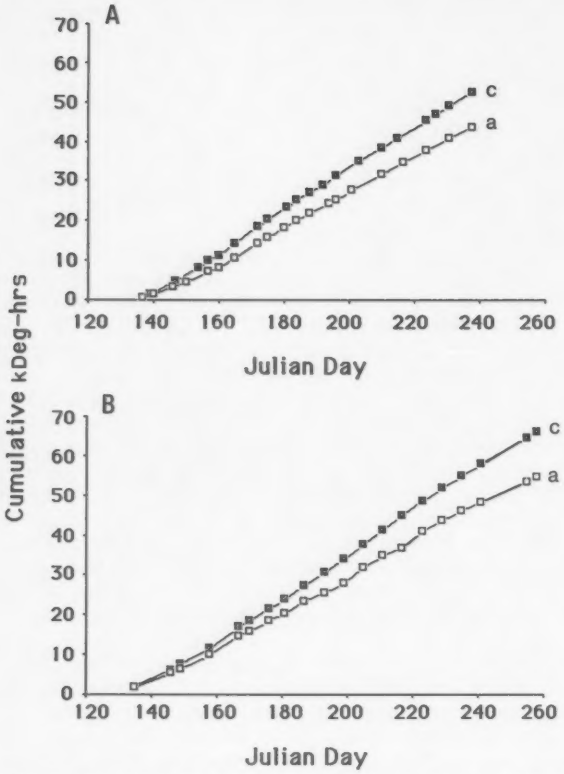


FIG. 2. Cumulative kilodegree-hours for heated channel "c" and ambient channel "a" in (A) 1983 and (B) 1984.

larval drift while the stream was overflowing the channels in early May, and through egg deposition by emerging insects from the general stream environment. Densities of larvae increased dramatically after spring emergence; thus, egg deposition appeared to be the most effective means of colonization.

To estimate how much variability occurred within treatments, hierarchical ANOVA was performed on the 1983 wing length data. The F probability estimates from channels nested within treatments (Table 1) indicated that the ambient channels "a" and "b" did not differ from each other, nor did the heated channels "c" and "d," with respect to estimates of body size. In 1984 the loss of heated channel "d" precluded this statistical approach, so values from the ambient channels "a" and "b" were pooled, as were the values from the two traps on heated channel "c." To provide an estimate of how well the two ambient channels replicated, a one-way ANOVA was conducted between ambient channels (Table 1), and for 1984 these results showed again that there was no difference between ambient channels with respect to estimates of body size.

Life History Parameters

Overall development rate was investigated for species which developed from egg or early instar to adult within the experimental channels. The ΔT between ambient and heated channels was 2.5 and 4°C for 1983 and 1984, respectively. The majority of the insects in this group developed more quickly in the elevated thermal regime — whether at 2.5 or 4°C above ambient

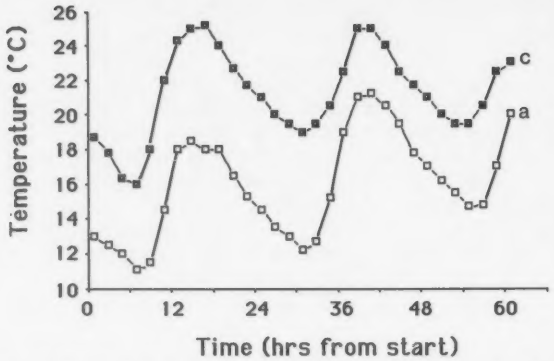


FIG. 3. Diel periodicity in temperature, starting at 2400, June 4, 1983, for heated channel "c" and ambient channal "a."

(Fig. 4). Fifty percent emergence occurred up to 39.1 d earlier (for *P. aviceps*) in the heated channel, but generally ranged between about 3 and 12 d earlier at the higher temperature (Table 2).

Insect emergence data plotted against physiological time (kilodegree-hours) rather than chronological time (Julian days) show one of three responses: (1) the variability in emergence between treatments (max D) is largely eliminated (e.g. *A. mallochi* '83, *C. aleta* '83, *N. fimbriatus* '83, '84, *R. distinctissimus* '84, *S. brevis* '84, and *S. venustum* '84, (2) the variability remains similar (e.g. *P. aviceps* '84), and (3) the variability actually increases (*P. lundbecki* '84) (Fig. 4). For most species, the maximum difference between relative cumulative emergence curves, and the probability they differ, decreased when the x-axis was kilodegree-hours. *Parametriocnemus lundbecki* was an exception, with max D increasing using the physiological time axis.

The response of adult body size to elevated temperature was surprisingly consistent. Regardless of functional group, most adults from the heated channels were smaller than those from the ambient channels (Table 1). The overall main effect of temperature was significant for 1984 when the ΔT was 4°C (ANOVA, $p < 0.0001$), although it was insignificant for 1983 when the ΔT was 2.5°C ($p = 0.076$). Most of the interaction terms were significant for both years, so overall main effects must be interpreted with caution. *Parametriocnemus lundbecki* and *S. brevis* decreased more in 1984 than in 1983. The estimated percent decrease in body weight ranged from 45.1% in *P. lundbecki* females to 2.4% in *C. aleta* males.

For five of the seven species, females decreased in size more than males (Table 1), and the interaction between sex and temperature was significant for both years ($p = 0.035$ and 0.003 for 1983 and 1984, respectively). One species, however, differed from the trend — *M. pedellus* females increased and males decreased.

The effect of the elevated temperature on reproductive potential was investigated in detail for four species. When ln ovary area was regressed against body size (ln wing length), no significant relationship appeared for *C. aleta*, *P. aviceps*, and *S. brevis* (Table 3). The partial regression coefficients are the proportion of variation in ovary size explained by wing length or egg area, after any intercorrelation between these variables has been removed. Only *P. lundbecki* showed a significant, but weak positive relationship between ovary size and body size

TABLE 1. Effect of the elevated temperature on insect wing length and estimated adult body weight.

Species	Year	Sex	Ambient	Heated	Probability no difference: between treatments[a]	Probability no difference: between channels-(within treatments)[b]	% difference in body size[c]
Predators							
Ablabesmyia mallochi	1984	F	7	30			−29.9
Ablabesmyia mallochi	1984	M	8	17	0.0465	0.8817	−11.3
Conchapelopia aleta	1984	F	29	31			−20.1
Conchapelopia aleta	1984	M	29	30	0.0264	0.5409	−2.40
Nilotanypus fimbriatus	1983	F	15	16			−14.3
Nilotanypus fimbriatus	1983	M	19	21	0.0912	0.0475	−14.4
Nilotanypus fimbriatus	1984	F	32	27			−15.1
Nilotanypus fimbriatus	1984	M	29	19	0.0051	0.6031	−16.5
Detritivores							
Microtendipes pedellus	1983	F	23	15			+31.1
Microtendipes pedellus	1983	M	27	30	0.6133	0.8552	−26.5
Parametriocnemus lundbecki	1983	F	14	8			+6.50
Parametriocnemus lundbecki	1983	M	7	3	0.8328	0.4673	−3.90
Parametriocnemus lundbecki	1984	F	37	31			−45.1
Parametriocnemus lundbecki	1984	M	25	34	0.0001	0.0677	−13.4
Polypedilum aviceps	1984	F	31	21			−34.5
Polypedilum aviceps	1984	M	24	18	0.0001	0.3635	−31.7
Stempellinella brevis	1983	F	27	35			−13.4
Stempellinella brevis	1983	M	34	24	0.0133	0.8254	−18.7
Stempellinella brevis	1984	F	32	30			−44.7
Stempellinella brevis	1984	M	37	31	0.0001	0.2405	−26.9

[a]Probability that wing length is the same for ambient and heated treatments. For 1983, analysis is based on nested ANOVA, with channels nested within treatment as the error term. For 1984, analysis is a fixed-effect, two-way ANOVA.

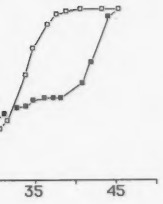
[b]Probability that the channels differ within a treatment. For 1983, analysis is a nested ANOVA. For 1984, analysis is based on a one-way ANOVA, comparing ambient channels "a" and "b" (one heated channel was lost).

[c]Percent difference is the difference in approximate body weight, $(1\text{-}W_{\text{heated}}/W_{\text{ambient}}) \times 100$, between ambient and heated channels, with body weight estimated by the expression $W = aY^b$ where W = insect weight, $a = 7.0 \times 10^{-7}$, Y = wing length, and $b = 5.83$. Coefficients were derived from data in Svennson (1975). Statistics were not based on this scale of measurement.

TABLE 2. Summer emergence statistics. Days between 50% emergence is horizontal deviation between relative cumulative emergence curves at the 0.5 mark, and max D is the maximum vertical deviation between curves. All cumulative emergence curves are significantly different ($p = 0.01$), unless noted as nonsignificant (ns). Probability values are given in table 2.4 in Rempel (1987).

Species	Year	Days between 50% emergence	Max D (Julian days)	Max D (kDeg-hrs)
Chironomidae				
Abebesmyia mallochi	1983	12.1	0.621	0.175 ns
Conchapelopia aleta	1983	8.6	0.384	0.238
Conchapelopia aleta	1984	7.4	0.179	0.238
Microtendipes pedellus	1983	1.1	0.317	0.500
Nilotanypus fimbriatus	1983	5.5	0.44	0.350
Nilotanypus fimbriatus	1984	9.0	0.371	0.263
Parametriocnemus lundbecki (pH 2)	1984	1.3	0.163	0.425
Polypedilum aviceps	1984	39.1	0.569	0.488
Rheotanytarsus distinctissimus	1984	7.6	0.477	0.200 ns
Stempellinella brevis	1984	3.6	0.231	0.180
Simuliidae				
Simulium venustum (pH 2)	1984	8.2	0.47	0.188 ns

A. mallochi '83
N= 141, 180
C. aleta '84
N= 258, 510
M. pedellus '83
N= 64, 89
RELATIVE CUMULATIVE ADULT EMERGENCE
CHRONOLOGICAL TIME
(Julian Days)
PHYSIOLOGICA
(kDeg-hr



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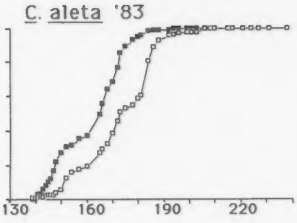
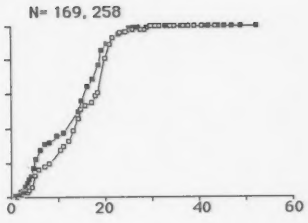
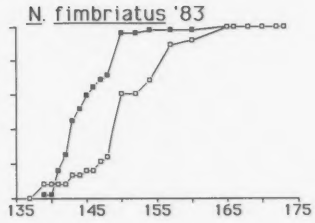
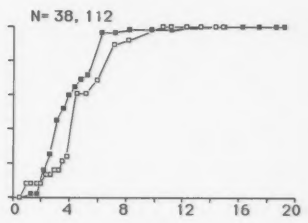
g-hrs)









CHRONOLOGICAL TIME
(Julian Days)

PHYSIOLOGICAL TIME
(kDeg-hrs)

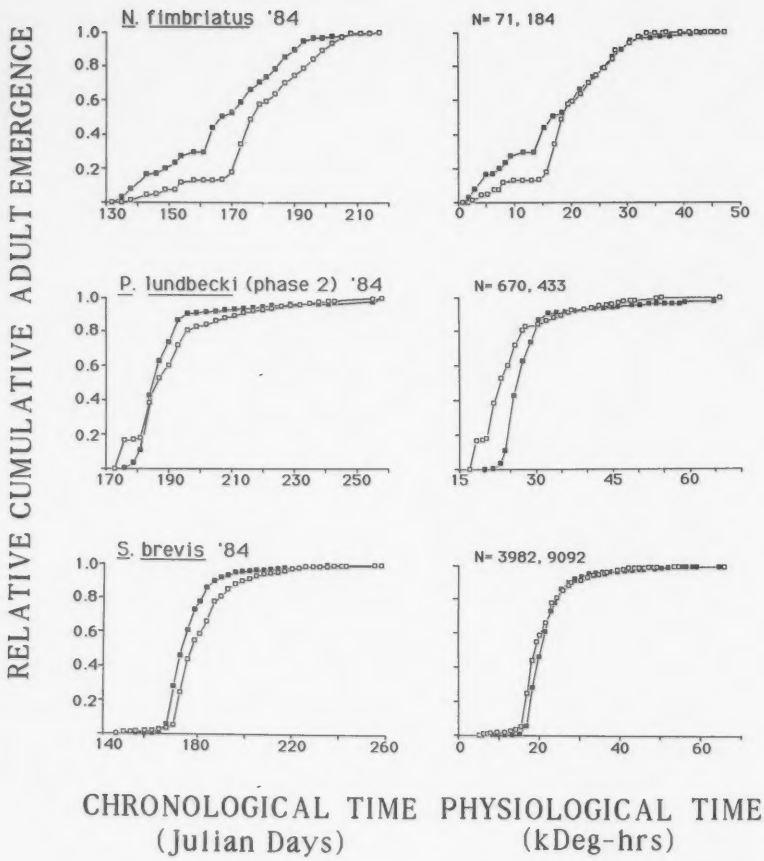
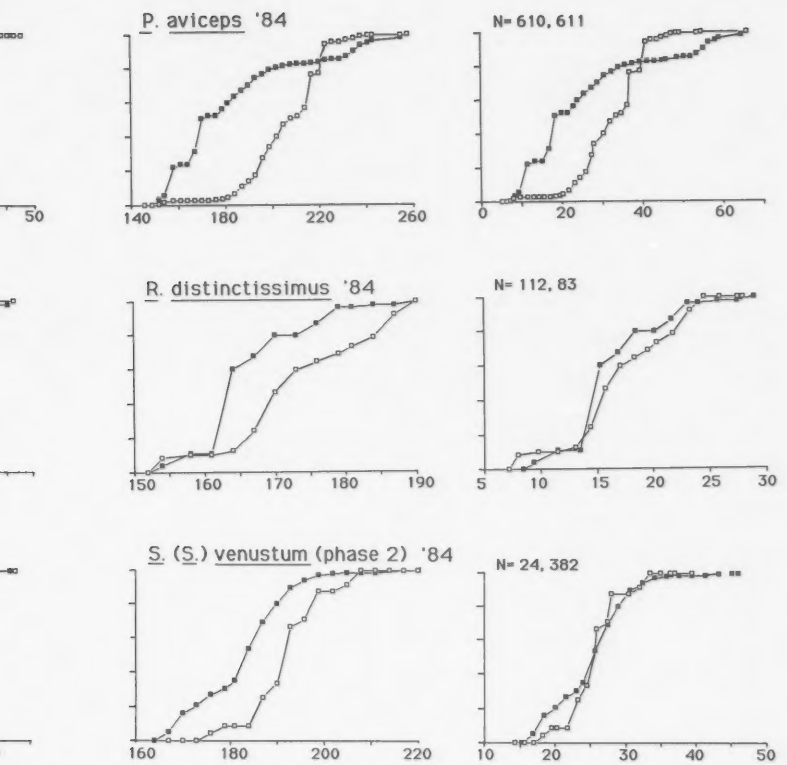


FIG. 4. Cumulative emergence curves. Ambient channel data are denoted by the ope
cumulative emergence from the sum of either the two ambient or two heated chan
channel. Each distribution is plotted in both chronological (Julian Days) and phys
Julian Day 141, 142; June 21 is 172, 173; and September 21 is 264, 265 in 1983 a



IME CHRONOLOGICAL TIME PHYSIOLOGICAL TIME
(Julian Days) (kDeg-hrs)

the open symbols and heated by solid symbols. For 1983, each curve is the relative
ed channels. For 1984, the heated curve is from the sum of two traps on the one
nd physiological (kDeg-hrs) time. "Phase" refers to emergence phase. May 21 is
1983 and 1984, respectively.

TABLE 3. Multiple and simple regression results of relationship between ln (ovary area) with ln (egg area) and ln (wing length).

Variable entered	Partial R^2	F	df	Probability $\beta \neq 0$	Multiple R^2	Probability $\beta_1, \beta_2 \neq 0$
Conchapelopia aleta						
ln egg area	0.524	16.49	1,15	0.0010		
ln wing length	0.022	0.67	1,15	0.4274	0.545	0.0040
Polypedilum aviceps						
ln wing length	0.232	3.01	1,10	0.1133		
ln egg area	0.228	3.79	1,10	0.0835	0.459	0.0629
Parametriocnemus lundbecki						
ln egg area	0.364	13.19	1,23	0.0014		
ln wing length	0.239	13.28	1,23	0.0015	0.604	0.0001
Stempellinella brevis						
ln egg area	0.571	10.64	1,8	0.0115		
ln wing length	0.039	0.706	1,8	0.429	0.610	0.0370

($r^2 = 0.24$). Thus, ovary size did not change with body size, or in the case of *P. lundbecki*, did so very slightly.

Discussion

The trend towards faster development at higher temperatures seems to be a general phenomenon in the aquatic Diptera we studied. In our simulation study (Rempel and Carter 1987), we found that accelerated development led to higher rates of population increase and equilibrium levels of abundance. This accelerated development is probably accounted for by the higher metabolic rates experienced in the elevated thermal regime. The response of accelerated development at higher temperatures (up to a limit) seems common among aquatic Diptera (Sweeney 1984). In this sense, the relationship is probably a "hard-wired" genetic characteristic of the order and not easily subject to natural selection. Butler (1984) used the term "exaptation" in opposition to "adaptation" to describe such characteristics.

If developmental speed is linked to metabolic rate, then the variability in emergence between treatments should be accounted for by the difference in physiological time. The measure of physiological time we used was cumulative degree-hours. The max D values based on the physiological time scale represent the degree to which development is linearly related to metabolic rate and provide an evaluation of the degree-day concept for explaining developmental variability. For most species, max D decreased when the x-axis was changed from Julian days to kilodegree-hours; thus, cumulative temperature accounts for some, and in many cases most, of the variability in emergence between channels. For one species, *P. lundbecki*, max D increased using the physiological time scale. For *P. lundbecki*, and those in which max D was only slightly reduced, a linear relationship between development rate and cumulative degree-hours does not adequately explain the regulation of development. A detailed study might reveal that a nonlinear function, perhaps exponential, best describes the relationship for this species.

Adult body size was consistently smaller among the detritivores in the heated channels, yet concurrent field and laboratory studies (Rempel and Carter 1986) demonstrated that autochtonous food resources (attached organic layers) were more developed and microbial activity and biomass associated with the detritus greater in the heated channels. Adult body size of predators, whose feeding rate may have increased with the elevated temperature, was also smaller in the heated water. The response to elevated temperature is cumulative and reflects the potential interaction of such parameters as altered food resources and metabolic rates; however, the general decrease in body size indicates that somatic growth may be acting independently of changes in the food resource. The question of how common or uncommon food limitation is in running waters is still largely unanswered. In a comparative ecological study of Ephemeroptera, Hawkins (1986) was unable to find conclusive evidence of food limitation to growth of individuals. However, he did suggest that populations may maintain equilibrium densities with habitats of varying food resources levels by balancing recruitment and emigration.

Relative independence of growth from food supply has also been recorded in lentic systems. McLaren (1965) noted that while growth of certain zooplankers is primarily a function of food supply, in other aquatic poikilotherms, size at any developmental stage is primarily a function of temperature, given sufficient food. It appears that the insects in this study are among those invertebrates whose growth and development is more a function of temperature than food supply, at least at temperatures and food resource levels encountered during the summer in this experimental stream.

There are some discrepancies in interpreting food limitation based on laboratory versus field experimental studies. In laboratory research, Sweeney et al. (1986) demonstrated that for *Soyedina carolinensis* (Plecoptera), diet primarily affected larval growth and adult size and temperature primarily affected overall development time. However, in a follow-up field experimental study, Sweeney and Vannote (1986) found that temperature had more importance than diet for larval growth and adult size and concluded that even small changes in temperature during larval growth could change the magnitude of larval growth. Although the two factors undoubtedly interact, in our field experiment the evidence indicates that temperature is of greater importance than diet in regulating growth.

The importance of adult body size in terms of population dynamics lies largely with the potential relationship between female body size and fecundity. The measure of reproductive potential used in this study is certainly less direct than the egg counts used to estimate reproductive potential of Ephemerop-

tera. Ovary area represents the area occupied by the developing follicles within the ovarioles. For the Chironomidae, egg development is finalized in the adult stage utilizing somatic energy reserves (Oliver 1968). There is no capacity to store eggs outside of the ovary after ovulation, although maturation of the second follicle in the ovariole may begin before the first egg batch is oviposited.

If only one egg deposition occurs, then ovary area would be a good measure of relative reproductive potential. However, if repeated ovarian cycles and oviposition occurs, then fewer somatic energy reserves in the smaller adults might limit further reproduction. It is not known how prevalent repeated reproduction is among the Chironomidae, although some arctic Chironomidae are known to have two ovarian cycles (Oliver 1968). For these chironomids, the second cycle was completed after 5–6 d, and the number of eggs produced was only about 15% of the first cycle; however, no oviposition of the second batch was observed in nature or captivity (Oliver 1968). These observations indicate that the first ovarian cycle is the most important cycle for reproduction and confirm that ovary area accounts for the major proportion of reproductive potential.

The interpretation of how temperature affects fecundity begins with the sexually dimorphic effects on body size. In most cases, females decreased in size more than males. At the same time, ovaries did not change in size at all with body size for three species, and did so only very weakly for one species. It appears that energy reserves are committed to vitellogenesis at the sacrifice of somatic tissue growth — the effect being comparatively larger ovaries in smaller individuals. Certainly, insects are capable of regulating the use of energy reserves and can redistribute the energy contained in reproductive and somatic tissue reserves in response to physiological conditions (Downer 1981).

This response is opposite to that reported for species of Ephemeroptera, where reproductive effort (ratio of reproductive reserves to somatic reserves) decreases with decreasing body size (e.g. Britt 1962; Rogers 1983; Sweeney 1978; Vannote and Sweeney 1980) and increasing temperature (Martin and Gates 1984). These apparent differences in response to temperature may be related to differences in reproductive physiology. In the Ephemeroptera, almost all internal somatic tissue in the adult is absorbed and used for egg development. Reduced somatic growth results in less available energy for conversion to eggs. In the Diptera, the adult female still retains considerable somatic reserves.

The sacrifice of somatic tissue to conserve fecundity has both advantages and disadvantages. For "*r*-selected" species, the capacity to produce large numbers of eggs results in a greater intrinsic capacity for population increase (see Rempel and Carter 1987). In a variable and unpredictable environment with high juvenile mortality, it is advantageous to maintain a high level of genetic diversity (Levins 1968; Labeyrie 1978). The creation of a large number of gene combinations (i.e. gametes) through sexual reproduction would help ensure this genetic variability within the deposited egg mass. In addition, if female mortality is affected by environmental variability (e.g. unpredictably harsh weather), then selection will favour "increased reproductive effort, larger clutches, and short-lived organisms" (Stearns 1976). In all these situations, maintaining reproductive potential at the expense of somatic reserves would be favoured.

On the other hand, fewer somatic reserves means that for nonfeeding females, less time is available for finding suitable egg-laying habitat and for waiting-out unsuitable weather for mating or laying eggs. With highly variable mortality in the juvenile stages resulting from environmental heterogeneity, selection of a suitable habitat is probably of great importance for the species (Butler 1984). Such conditions would favour "bet-hedging" in which the reproductive period is extended (Murphy 1968; Stearns 1976), i.e. repeated ovarian cycles and extended egg laying. Loss of somatic energy reserves may thus impose a substantial cost on the species' fitness, although extended egg hatching is an alternative option.

These interacting ecological factors probably all strongly influence the selective pressures on reproductive potential and adult body size. A precise evaluation of which factors have most weight is difficult, at best. However, the simulation model (Rempel and Carter 1987) predicts that in terms of colonization ability and equilibrium population abundance, accelerated development can potentially make up for a reduction in fecundity, and this is substantiated by the significantly greater abundance of Diptera in the heated channels (Rempel and Carter 1987). In balance, the overall analysis indicates a resistance to thermal elevation, leading to a kind of population stability, at least within the thermal range of the experiment. For these small, opportunistic species, reproductive potential is at least partially conserved, and population survivorship enhanced, when temperature is elevated 4°C.

The enhanced population survivorship resulting from accelerated growth provides additional compensation to insects that develop more quickly, but grow less in size during the summer. It is an important population effect not considered in the thermal equilibrium hypothesis of Vannote and Sweeney (1980). The aquatic Diptera, especially some of the multivoltine Chironomidae, are able to effectively colonize and utilize temperate stream resources in all seasons (Rempel and Harrison 1987). The ability of some species in the group to compensate for seasonal changes in the thermal regime, in effect, adopting a thermal-generalist strategy, may be an important factor explaining their ubiquitous presence in stream ecosystems.

Acknowledgements

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Phosphate Requirement, Photosynthesis, and Diel Cell Cycle of *Scenedesmus obliquus* Under Fluctuating Light

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Shin, C. N. G-Y. Rhee, and J. Chen. 1987. Phosphate requirement, photosynthesis, and diel cell cycle of *Scenedesmus obliquus* under fluctuating light. Can. J. Fish. Aquat. Sci. 44: 1753–1758.

The effect of light fluctuation (0.06 Hz) on P requirement, photosynthesis, and the diel cell-division cycle was investigated in *Scenedesmus obliquus* in a chemostat under a 12 h day: 12 h night cycle. P requirement was much less under oscillating than under constant daylight of the same photon flux density. However, cell chlorophyll *a* was significantly higher, indicating an increased N requirement. There was little difference in photosynthetic efficiency (the slope of the photosynthesis–light regression) between oscillating and constant light, but photosynthetic capacity was higher in fluctuating light. Cell C was also higher. A strong diel rhythmicity in steady-state cell numbers was observed with little phase difference between oscillating and constant light. Although steady-state cell numbers under P limitation were significantly higher under fluctuating light, there was no difference in instantaneous growth rates and their diel distribution. At a dilution rate of $0.6 \cdot d^{-1}$, cell death occurred at an average rate of $-0.56 \cdot d^{-1}$ between 4 h before and 5 h after the onset of the dark period.

Les auteurs ont étudié les effets de la fluctuation de l'éclairement (0,06 Hz) sur les besoins en P, la photosynthèse et le cycle nycthéméral de la division cellulaire chez *Scenedesmus obliquus*. Les essais ont été réalisés en chémostat et le cycle jour/nuit était de 12/12 h. Les besoins en P étaient de beaucoup inférieurs en régime oscillatoire qu'en condition d'éclairage de jour constant, ceci à la même densité de flux photonique. La teneur en chlorophylle *a* cellulaire était cependant plus élevée de façon significative, ce qui indique une augmentation des besoins en N. L'efficacité photosynthétique (pente de la régression photosynthèse–lumière) présentait peu de différences entre les régimes d'éclairement oscillatoire et constant, mais la capacité photosynthétique était plus élevée en régimes d'éclairement fluctuant. La teneur en C cellulaire était aussi plus élevée. Une forte rythmicité nycthémérale du nombre de cellules à l'état d'équilibre a été notée; il y avait un léger écart de phase entre les régimes d'éclairement oscillant et constant. Le nombre de cellules à l'état d'équilibre (limitation par P) était significativement plus élevé en régimes d'éclairement fluctuant, mais il n'y avait pas d'écart entre les taux de croissance instantanés et leur distribution nycthémérale. Au taux de dilution de $0.6 \cdot j^{-1}$, la mort cellulaire survenait à un taux moyen de $-0.56 \cdot j^{-1}$ au cours de la période s'étendant de 4 h avant à 5 h après le début de la période d'obscurité.

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The underwater light field of the euphotic zone is temporally dynamic, changing in seasonal and diel cycles and at frequencies as short as a fraction of a second. The frequency of changes within the diel period is largely associated with vertical mixing of the water column and shifts in meteorological conditions, such as cloud cover and wind speed.

The fluctuation of photic environments has profound effects on many physiological processes in phytoplankton. The diel cycle, for example, entrains cell division, photosynthesis, cellular biosynthesis, and metabolism (Chisholm 1981; Rhee et al. 1981; Sournia 1974). To fluctuations occurring at frequencies of several hours or longer, which are frequently associated with the vertical movement of water, organisms adapt with little time lag with changes in pigment concentrations or in the number and/or size of the photosynthetic unit (Perry et al. 1981; Falkowski 1984; Prezelin 1981; Richardson et al. 1983). To fluctuations with time scales of seconds to minutes, which are typical under passing clouds, organisms respond with short-term adaptive mechanisms, such as those involving fluorescence yield and redox carriers in the photosynthetic electron-transport system (Gallegos et al. 1980; Marra and Heinemann 1982).

Light at high frequencies, generated by surface waves and ranging from 0.01 to 10 Hz (Snyder and Dera 1970; Dera et al. 1975), appears to influence both photosynthesis and growth through yet-unknown mechanisms. The growth rate of *Chlorella* sp. decreased with increasing frequencies from 15 to 1000 Hz, and only at the highest frequency was the growth rate identical to that obtained under steady light (Phillips and Myers 1954). Within a photocycle of 40 s, the growth rate of *Chlorella* also increased with the ratio of light:dark periods due to

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decreasing requirements for maintenance energy (Lee and Pirt 1981). Photosynthetic responses also appear to be affected. Walsh and Legendre (1982) reported that both photosynthetic efficiency, i.e. the slope of the photosynthesis–light regression, and photosynthetic capacity varied with changes in light frequencies, but there was no pattern in the changes. Walsh and Legendre (1983) found the highest efficiency at 10 Hz with no change in capacity.

In the natural environment, phytoplankton populations are exposed not only to dynamic light regimes but also to various environmental stresses, notably nutrient limitation. Subsaturating light intensities tend to increase nutrient requirements (Rhee and Gotham 1981b). It has been unclear, however, how fluctuating light affects nutrient limitations or requirements and whether the diel cell cycle may be affected by shorter frequencies of light fluctuation.

Our present work has investigated whether daylight flicking (0.06 Hz) has any effect on the phosphate requirement and on the diel cycle of cell division and photosynthesis in the freshwater alga *Scenedesmus obliquus*.

Materials and Methods

Scenedesmus obliquus, isolated and used in previous studies by Rhee (1973, 1978, 1980) and Rhee and Gotham (1981a, 1981b), was grown in a defined inorganic medium (Guillard and Lorenzen 1972) with the concentration of P reduced to 2 μM for P limitation. This organism was cultured in a chemostat (working volume 500 mL) at a fixed dilution rate ($0.60 \cdot d^{-1}$) under a 12 h light : 12 h dark cycle in a constant-temperature room (18°C). Light from a quartz–halogen lamp was directed at the culture through a heat sink, made of two transparent Plexiglas layers between which cold water was circulating, and then through two polarizing filters (3M Co., 30 × 30 cm). A rotating filter driven by a motor–pulley system generated a sinusoidal fluctuation of light (0.06 Hz). To provide steady light of the same photon flux density, the polarizing axes of the two filters were aligned in a fixed position, and the light intensity was reduced by half with a neutral filter, resulting in an average intensity inside the culture vessel of 216 $\mu E \cdot m^{-2} \cdot s^{-1}$.

When the culture reached a steady state, the overflow was connected to a refrigerated (0°C) fraction collector covered with aluminum foil, and hourly samples were collected. Part of each sample was used for cell counting and chlorophyll determination. The rest was centrifuged, and the supernatant and cell pellets were stored at −23°C for further analyses. Samples were collected for at least 3 consecutive days and values presented are their averages.

Photosynthesis was measured at 2:00 p.m. as $NaH^{14}CO_3$ incorporation with steady-state cells siphoned out from the culture vessel. They were subdivided into 24 samples and exposed in duplicate to "cool white" fluorescent lights of various intensities for 20 min. Different intensities were obtained using neutral filters in combination with the adjustment of distance between the sample and light. Photosynthetic efficiency and capacity were estimated according to Jassby and Platt (1976).

Quantum efficiency (micromoles C fixed/microeinsteins absorbed) was measured in an integrating sphere (Welshmeyer and Lorenzen 1981) modified as follows. The volume was reduced to 12 mL. Illumination in the sphere was provided through an optical fiber connected to a microscope illuminator and absorption was determined through another optical fiber, one end of which was tightly attached to a Li-Cor quantum sensor and the other end to the sphere. A test of effectiveness of the sphere using $BaSO_4$ in distilled water confirmed that absorption measurements were little affected by scattered light.

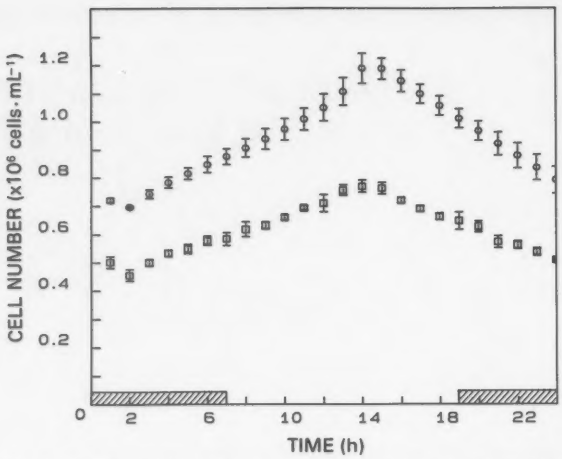

FIG. 1. Diel distribution of steady-state cell numbers under oscillating (○) and steady light (□)under a 12 h light : 12 h dark cycle.

Chlorophyll *a* was analyzed after extracting with chloroform–methanol according to Wood (1985). Cell P was determined after persulfate oxidation to orthophosphate (Menzel and Corwin 1965) and also calculated from the difference in the P level in the reservoir and culture at steady state. Total cell C was measured on a Beckman carbon analyzer (model 915B). Cell numbers were counted using a hemacytometer.

The instantaneous growth rate, $\mu(t)$, was computed as $D + (\ln dX)/dt$, where D is the dilution rate, X is cell number, and t is time.

Results

Cell division, as indicated by changes in cell numbers, showed a strong diel periodicity under both oscillating and steady light at the same photon flux density. The highest cell number occurred 8 h after the subjective dawn (Fig. 1).

The instantaneous growth rates, $\mu(t)$, calculated at hourly intervals, showed little difference between steady and oscillating lights; both the absolute value of $\mu(t)$ and its phase restriction were identical. Cell division occurred between 0100 and 1500 and the two maxima of $\mu(t)$ occured at the beginning and end of this period (Fig. 2). After the second maximum, $\mu(t)$ decayed exponentially. This decay could be approximated by a simple first-order function, and the change in cell number could be expressed as a function of $\mu(t)$, as previously reported for *Fragilaria crotonensis* and *Asterionella formosa* (Gotham and Rhee 1982):

$$(1) \quad \mu(t) = \mu_p\{2 \exp [(\tau - t)/\sigma] - 1\}$$

where μ_p is a maximum value of $\mu(t)$ at the second burst at time τ and σ is the time constant for the decay. Cell numbers during the decay was related to $\mu(t)$ by the equation

$$(2) \quad X(t)/X_0 = \exp\left[\int_0^t \mu(t)dt - Dt\right]$$

where $X(t)$ is the cell number at time t, X_0 is the number at time 0

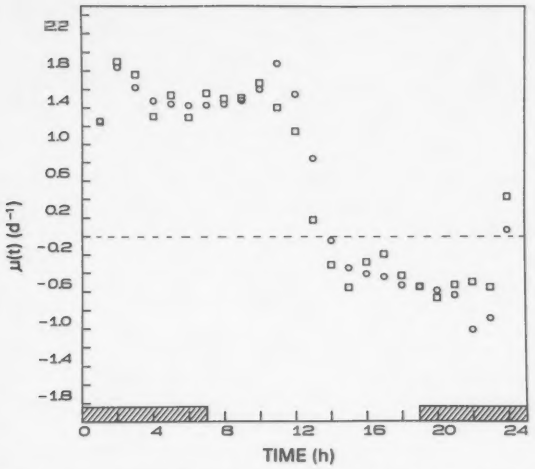

FIG. 2. Instantaneous growth rates, $\mu(t)$, under oscillating (○) and steady light (□).

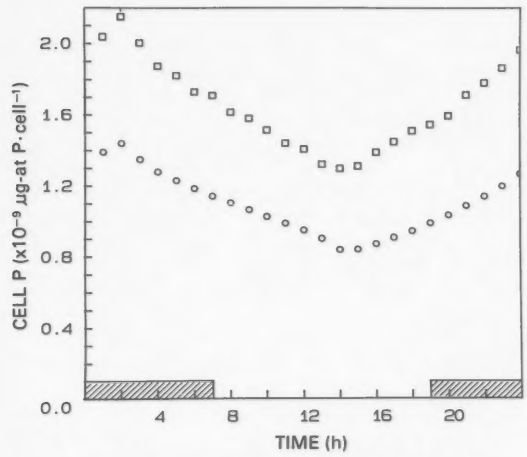

FIG. 3. Cell P under oscillating (○) and steady light (□).

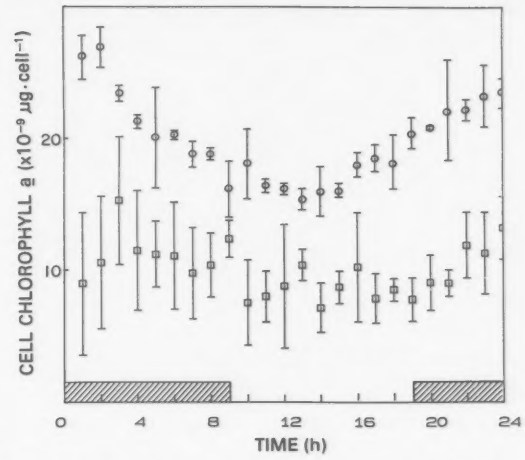

FIG. 4. Cell chlorophyll *a* under oscillating (○) and steady light (□).

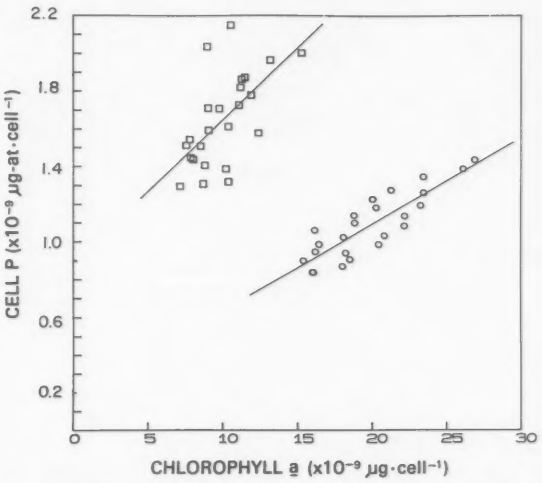

FIG. 5. Cell chlorophyll *a* vs. cell P under oscillating (○) and steady (□) light.

or at the trough of oscillation, and D is the dilution rate ($0.60 \cdot d^{-1}$). The declines of cell numbers from 1400 to 2400 were greater than could be explained by simple dilution of the culture and indicated negative growth rates, or cell death, at an average rate of about $-0.56 \cdot d^{-1}$ (Fig. 2). No significant change in cell volume or colony size was observed under the microscope.

Cell P (Fig. 3) and chlorophyll *a* (Fig. 4) concentrations also showed a strong diel periodicity with little difference in phase between constant and fluctuating light. Since the steady-state cell number was significantly higher under oscillating than under steady light at the same dilution rate ($0.60 \cdot d^{-1}$; Fig. 1) and no residual P was detectable in the culture medium, cell P was much lower under oscillating light throughout the diel cycle. In contrast, the cell chlorophyll *a* was significantly higher under fluctuating light, an increase similar to that in low-light-adapted cells.

Since there is a strong correlation between cell N and chlorophyll *a* concentrations (Rhee and Lederman 1983; Wynne and Rhee 1986), this higher pigment concentration indicated an increase in cell N. Thus the cell P decreased while the cell N appeared to increase under oscillating light which would result in a sharply higher N:P ratio.

A positive correlation was also found between diel changes in cell P and chlorophyll *a* ($P < 0.001$) under both fluctuating and constant light. The slope (micrograms Chl *a*/micrograms P) was steeper under steady (0.076 ± 0.021) than under oscillating light (0.046 ± 0.006), indicating a lower cell P : chl *a* ratio (Fig. 5).

When photosynthetic efficiency and capacity were estimated on a per-cell cell basis, both parameters were much greater for cells grown under oscillating than under constant light (Fig. 6a). On a per-chlorophyll *a* basis, however, no significant difference in the efficiency was seen ($P < 0.10$, ANCOVA), although the capacity was still higher in fluctuating light (5.33 ± 0.29 vs. 4.55 ± 0.20) (Fig. 6b).

A diel periodicity was not observed in cell C (Fig. 7). However, this seeming absence of periodicity probably stemmed

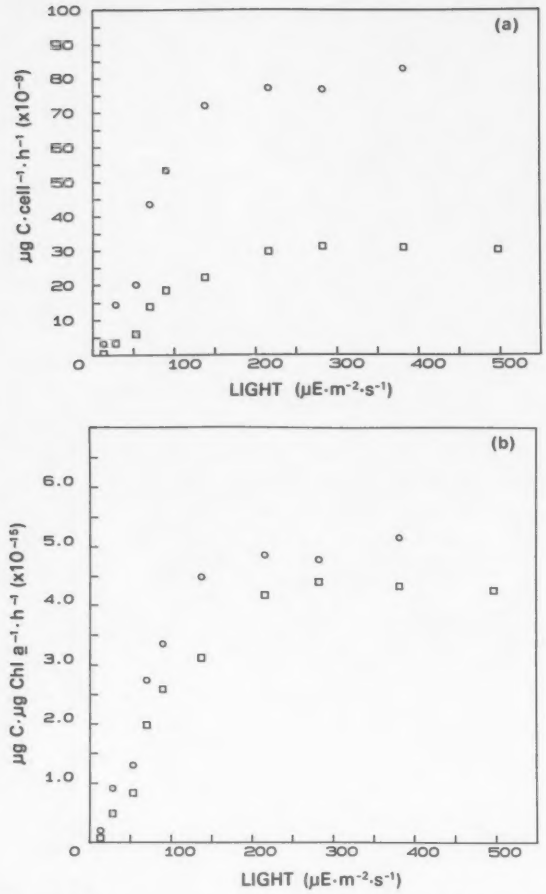

FIG. 6. Photosynthesis (a) per cell and (b) per chlorophyll *a* under oscillating (○) and steady light (□).

from the scatter of data combined with a small amplitude of cell C oscillation, because cell C could not remain unchanged during cell division in the dark between 0000 and 0700. It is possible that during this period, cells utilized dissolved organic C resulting from cell death and lysis. However, the production of dissolved organic C, which could be estimated as the area of negative $\mu(t)$ between 0000 and 0700 in Fig. 2, was insufficient to provide C required to maintain a constant level for dividing cells in the dark. Thus, it is likely that there was a diel variation in cell C, although dissolved C could have dampened the amplitude of the variation. The average cell C over a 24-h period was significantly higher ($P < 0.05$, *t*-test) under fluctuating than under constant light.

Quantum efficiency (micromoles C fixed/microeinsteins absorbed) was significantly higher in cells grown under oscillating light (0.092 ± 0.020) than under steady light (0.062 ± 0.014) at an incident light intensity of 3.6 $\mu E \cdot m^{-2} \cdot s^{-1}$. No clear pattern of diel changes could be determined.

Discussion

An especially striking result of this study is the finding that cells under fluctuating light contained significantly lower concentrations of P and higher concentrations of chlorophyll *a* and C than cells under constant light of the same photon flux density. The maximum growth rate (μ_{max}) was also higher under fluctuating than under constant light (1.50 vs. 1.36·d^{-1}). Therefore, for cells growing at the same μ, the relative growth rate (μ/μ_{max}) was lower under light fluctuation.

A question might then be raised whether the changes in cell composition were associated with the lower relative growth rate, rather than light conditions. Previous studies of the same organism under P or N limitation (Rhee 1973; 1978) and light and temperature stresses (Rhee and Gotham 1981a, 1981b), as well as the report of Goldman (1981) on temperature effects on marine diatoms, have shown that cell C, N, P, and pigment contents decrease with relative growth rate. Thus, if the cellular changes under fluctuating light were a result of lower relative growth rates, cell chlorophyll *a*, P, and C contents should have been lower under fluctuating than under constant light. However, cell chlorophyll *a* and C contents were higher, while cell P was lower. Therefore, the changes in cell composition were due to fluctuating light and were not related to relative growth rate.

The changes were also not related to adaptive responses to light conditions, since low cell P is a characteristic of light saturation (Rhee and Gotham 1981b) and high chlorophyll *a* level is a characteristic of adaptation to low light.

Since total cell N is proportional to chlorophyll *a* concentrations under various light conditions (Rhee and Lederman 1983; Wynne and Rhee 1986), the high pigment concentration at this frequency indicates a high total cell N. With higher cell N coupled with lower cell P, the cell N:P ratio of cells under fluctuating light would then be sharply higher than that under constant light. If this increase is an adaptive mechanism, the optimum N:P ratio, i.e. the N:P ratio at which the transition between N and P limitation occurs, may also increase to maintain the growth rate.

It is unclear whether the change in cellular composition is frequency dependent in *S. obliquus*. In *Dunaliella tertiolecta*, chlorophyll *a* concentrations were higher at 0.1 and 10 Hz than at steady light but were the same at 1.0 Hz (Qu'guiner and Legendre 1985).

Photosynthetic efficiency in *S. obliquus*, as in many other species (Sager and Giger 1980), showed little difference between oscillating and constant light. However, in *D. tertiolecta* the efficiency was higher under fluctuating light (Qu'guiner and Legendre 1985). Photosynthetic capacity in *S. obliquus* was significantly higher under fluctuating light as it was in *D. tertiolecta*.

Under oscillating light photosynthetic efficiency in *S. obliquus* changes little but chlorophyll *a* was higher, resembling the phenomenon of shade adaptation by increasing photosynthetic unit size (Falkowski 1984; Prezelin 1981; Richardson et al. 1983). However, the higher photosynthetic capacity, indicating increased enzymatic rates in electron transport and/or CO_2 fixation, was a phenomenon contradictory to shade adaptation. Some green algae are known to decrease their enzyme activities at low light (Prezelin 1981). Therefore, the photosynthetic characteristics under oscillating light indicate, as the cell P and chlorophyll *a* contents did, that the cellular responses to fluctuating light are not the same physiological adjustments as those involved in adaptation to light intensity.

It was unclear why the quantum yield was lower in cells grown in steady light than in oscillating light. One possibility is absorption of some light by nonphotosynthetic pigments. In the present work, pigments other than chlorophyll *a* were not

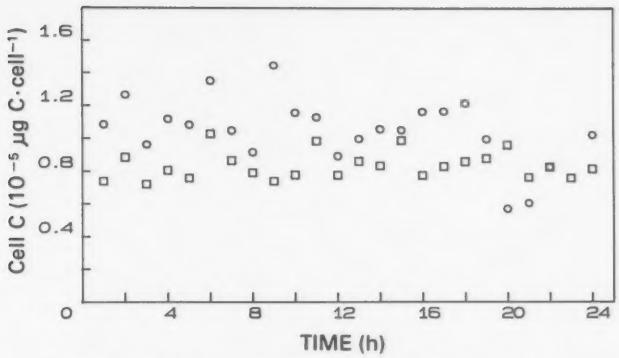

FIG. 7. Cell C under oscillating (○) and steady light (□).

determined, but in *D. tetiolecta*, pigment composition was little affected by oscillating light (Qu'guiner and Legendre 1985). Other possibilities include differences in the ratio of RuBP carboxylase/oxygenase and photorespiration, in light-dependent utilization of ATP and NADPH for cellular functions, and in electron transport occurring through a cyclic path.

Cell death is well known at slower growth rates (Rhee 1980), but we were surprised to find negative growth during a certain part of day in cells growing at the relatively high daily average growth rate ($0.6 \cdot^{-1}$). Based on earlier data of maximum growth rate (μ_{max}) under constant light, this daily average growth rate is equivalent to a relative growth rate (μ_{max}) of 0.44. The negative growth was due to P limitation, since it was not observed in a nutrient-sufficient turbidostat. The instantaneous death rate and its phase restriction were identical for constant and oscillating light. However, there may have been no phase restriction: death may have occurred throughout the 24-h period but may have been masked by high growth rates during cell division. In that case, the instantaneous growth rate during cell division should have been higher by the extent of the death rate. Apparently, cell death resulted in lysis, since $\mu(t)$ values were based on total microscopic cell counts. Morphological evaluation under light microscope revealed no nonliving cells.

In nature the light frequency used in our present work is associated with the surface waves, which focus and defocus light in cycles with very short periods, ranging from 0.01 to 10 Hz (Dera and Gordon 1968; Snyder and Dera 1970; McFarland and Munz 1975). The irradiance can change two- to threefold, but this change decreases with depth as the focusing becomes less effective in relation to other optical phenomena caused by wave movements. The maximum amplitude occurs at a certain depth below the surface because of light attenuation and the focusing effect (Dera et al. 1975). Our present results suggest that fluctuating light in the upper euphotic layer not only enhances light-saturated photosynthesis and biomass production, but may also alter the degree and/or kind of limiting nutrients. Nutrient limitation in the euphotic zone thus appears to be a complex phenomenon involving responses not only to light intensity (Rhee and Gotham 1981b; Wynne and Rhee 1986) and quality (Wynne and Rhee 1986), but also to the frequency of fluctuation.

For mass culture of algae for biomass production, culture systems are engineered to provide oscillating photic conditions for higher photosynthetic efficiency and faster growth (e.g. Laws et al. 1983; Markl 1980; Lee and Pirt 1981; Livansky 1979). Our results indicate that for maximum yield the system must also take into consideration special nutritional requirements which seem to depend on the frequency of light oscillation.

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Latitudinal Influences on the Depths of Maximum Colonization and Maximum Biomass of Submerged Angiosperms in Lakes[1]

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Duarte, C. M., and J. Kalff. 1987. Latitudinal influences on the depths of maximum colonization and maximum biomass of submerged angiosperms in lakes. Can. J. Fish. Aquat. Sci. 44: 1759–1764.

Both water transparency and lake latitude influence the depths of maximum biomass (Z_b) and maximum depth of colonization (Z_c) of submerged plants. The differences in the depth distribution of plants in lakes differing in water transparency become more pronounced as latitude decreases. Changes in transparency in low-latitude lakes should result in greater changes in macrophyte cover than similar changes in lakes at higher latitudes. The maximum depth of colonization appears to be largely a function of water transparency, whereas the depth of maximum biomass is best related to latitude. Relationships developed here allow better predictions of Z_c and Z_b for individual lakes than were possible before.

La transparence des eaux et la latitude influent sur la profondeur de la biomasse maximale (Z_b) et la profondeur maximale de colonisation (Z_c) des plantes lacustres submergées. Les écarts de la distribution des plantes en fonction de la profondeur des lacs de transparence différente s'accroissent à mesure que la latitude décroît. Une modification de la transparence de l'eau de lacs de faible latitude devrait avoir une plus grande influence sur la couverture de macrophytes comparativement à des lacs situés à des latitudes plus grandes. La profondeur maximale de colonisation semble être en grande partie fonction de la transparence de l'eau tandis que la profondeur de la biomasse maximale est plutôt fonction de la latitude. Les auteurs ont établi des relations qui permettent de mieux prévoir les valeurs des paramétres Z_c et Z_b dans le cas de lacs déterminés.

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Recent work has demonstrated that water transparency is closely related to the depth of maximum colonization of submerged macrophytes (Z_c, Hutchinson 1975, p. 414; Spence 1976; Chambers and Kalff 1985; Canfield et al. 1985; Vant et al. 1986; Dale 1986) and weakly related to the depth at which the maximum macrophyte biomass is found (Z_b, Chambers and Kalff 1985).

The models predicting Z_c provide a basis for the prediction of changes in the area colonized by the submerged macrophytes as a consequence of changes in water transparency (Canfield et al. 1985). The importance of the prediction of the depth where the maximum biomass of submerged plants occurs lies in that this depth separates a zone of light-limited plant growth from a shallower area where light levels are less important (Spence 1982). Further, Z_b also determines the underwater space available for growth, which may limit the maximum biomass possible (e.g. Lind and Cottam 1969). Because the constraints on plant growth above and below Z_b appear to differ (Spence 1982), the distinction between the two zones Z_b should simplify the study of the relationship between plant growth and habitat conditions. Consequently, the study of the factors influencing Z_b are as important as the study of the factors determining Z_c.

Existing relationships between Z_c and water transparency differ (cf. Vant et al. 1986), suggesting regional differences among them, while the weak correlation between Z_b and water transparency (i.e. Chambers and Kalff 1985) suggests the influence of other factors. One reason for the scatter and regional variability of the relationships based on Secchi depth may be that, by itself, water transparency reflects only the proportion of surface light within the water column, whereas macrophyte response is influenced by the amount. Additionally, Dale (1986) showed that the decrease in temperature with depth also restricts the depth of maximum colonization, even where water clarity would allow growth below the thermocline. Because both temperature and incoming irradiance are largely a function of latitude, equally transparent lakes at low latitudes should have higher underwater irradiance and temperature than those at higher latitudes. Thus, both Z_c and Z_b should be deeper in lakes at lower latitudes.

The goals of this study are (1) to test whether the latitude of a lake affects the maximum depth colonized by the plants and the depth where the maximum biomass occurs, (2) to quantify these effects, and (3) to examine the relative contributions of light penetration and geographical position in the determination of the depth distribution of submerged plants in lakes.

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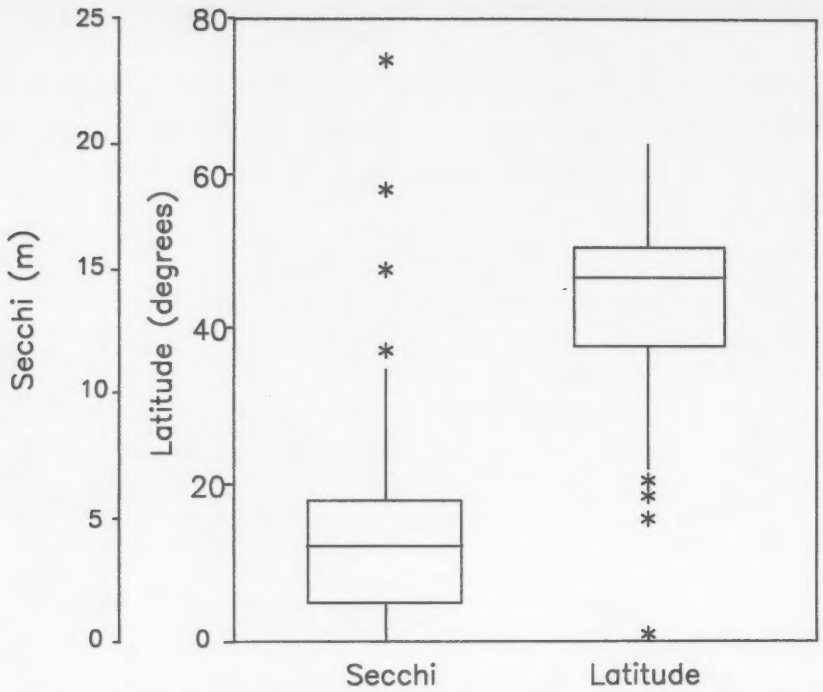

FIG. 1. Box plots showing the distributions of latitude and Secchi depth for the lakes in our data set. The middle line in the box is the median, the margins of the box are the 50% percentiles, and the bars extend to the 95% percentiles. The asterisks represent observations outside the 95% percentiles.

Methods

Previous determinations of Z_c and Z_b for submerged angiosperms were dominated by temperate data (Chambers and Kalff 1985; Canfield et al. 1985; Dale 1986; Vant et al. 1986). We compiled a data set that is more balanced with respect to latitude by obtaining data on Z_b, Z_c, and Secchi depth for (a) subtropical and tropical lakes in the published literature (Brown 1975; Milbrink 1977; Baas Becking et al. 1959; Howard-Williams et al. 1986), (b) the subtropical Florida lakes in Canfield et al. (1985), (c) the data in Chambers and Kalff (1985), (d) the Ontario lakes in Dale (1986), for which the Z_c for angiosperms is provided, and (f) the data in Duarte et al. (1986) not contained in the other data sets. The number of observations of Z_b was expanded by sampling lakes Hertel and Memphremagog (Quebec), Lake George (New York), and six Florida lakes, for which Z_b was determined as in Chambers and Kalff (1985).[3]

Water transparency was determined with the use of a 20-cm Secchi disc. Light readings given as extinction coefficients (k, per metre) were converted to Secchi depth values (S_D, metres) by assuming that $S_D = 1.47/k$ (Walker 1982), where k was obtained from the percent surface irradiance, I_z, at the depth of macrophyte growth, z, using the equation

$$(1) \quad k = \ln (100/I_z)/z.$$

Similarly, I_z was calculated as $I_z = 100\ e^{(-1.47zk)}$, where k was calculated as $1.47/S_D$ (Walker 1982) when light was reported as Secchi depth.

Relationships between the depth distribution of the plants, water transparency, and lake latitude were then modelled by use of regression analyses. The precision of the equations was indicated by their coefficent of determination (r^2) and the standard error of the estimates ($SE_{est.}$). The relative contribution of different independent variables to the variance explained in multiple regression was represented by their partial F values. When necessary, dependent variables (Z_c and Z_b) were transformed to meet the statistical requirements of linear regression, whereas the independent variables (latitude and water transparency) were transformed to maximize predictive power following Box and Tidwell (1962).

Results

The 164 lakes in the data set covered wide ranges of water transparency and latitude (Fig. 1). The latitudinal position of the lakes was approximately normally distributed, with its average at 42° (Fig. 1). The distribution of Secchi depths indicates that most lakes in the data set are mesotrophic (i.e. S_D between 2 and 6, Fig. 1). Most lakes are from Europe (45) or North America (94), but the data set also includes lakes from New Zealand (15), Australia (2), Asia (2), South America (2), and Africa (4). The ranges in Secchi depth and latitude provide a data set with wide ranges of Z_b (range 0.8–7.0 m, $N = 45$) and Z_c (range 0.0–18.0 m, $N = 160$).

[3]A complete data set is available at a nominal cost from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

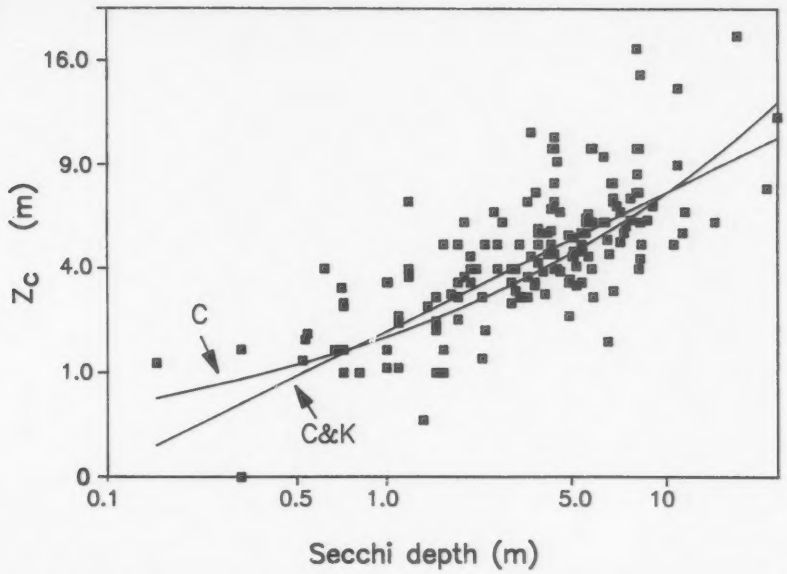

FIG. 2. Relationship between the depth of maximum colonization (Z_c) of aquatic angiosperms and the Secchi disc transparency. The lines illustrate the fit of the equations by Canfield et al. (1985) (C) and Chambers and Kalff (1985) (C&K) to our data.

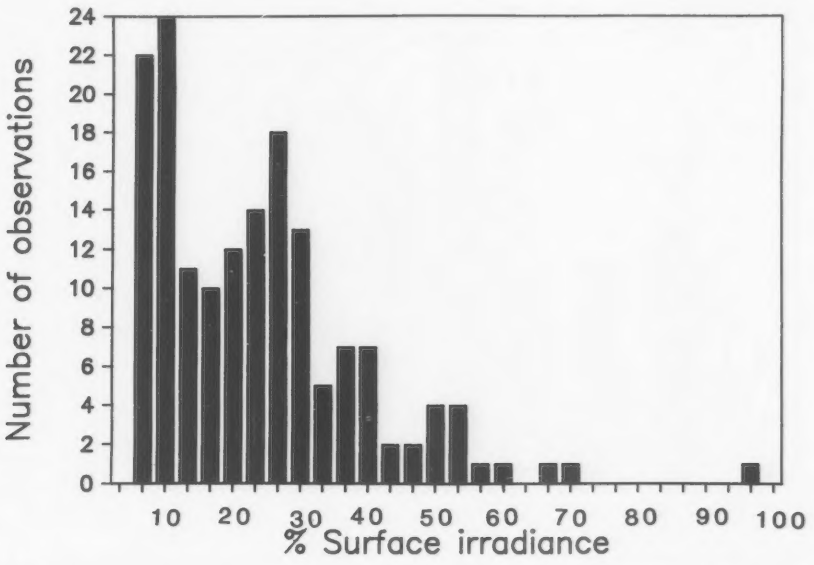

FIG. 3. Frequency distribution of the percent surface irradiance received at the maximum depth where macrophytes grow (Z_c).

Depth of Maximum Colonization

The relationship between the maximum depth of colonization and water transparency for the available data is (Fig. 2)

$$(2)\quad Z_c^{0.5}(\text{m}) = 1.51 + 0.53 \ln S_D(\text{m})\ r^2 = 0.51;\ N = 160;\ P < 0.0001;\ \text{SE}_{(\text{est.}^{0.5})} = 0.46.$$

This suggests that the degree of light penetration determines the maximum depth of colonization. This interpretation is supported by the relatively narrow range of irradiance levels at which Z_c occurs (Fig. 3). The irradiance received at Z_c is less than 30% of surface irradiance for most (i.e. 78%) of the observations (Fig. 3). Nevertheless, variation in both Z_c (for a given transparency) and in the percent surface irradiance received at Z_c (Fig. 2 and 3) is substantial. According to our hypothesis, this variation should be partially attributable to differences in latitude among lakes. This can be tested by examining the relationship between the percent surface irradiance received at

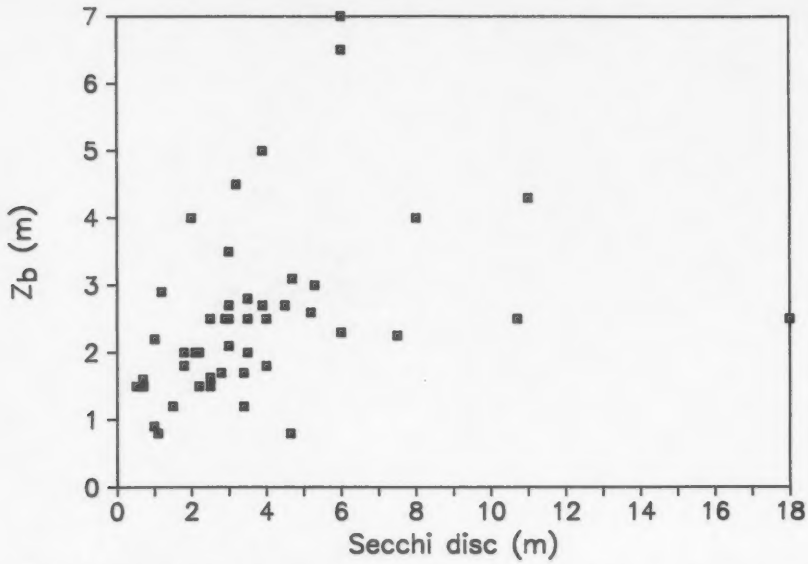

FIG. 4. Relationship between the depth where the maximum biomass of submerged angiosperms occurs (Z_b) and the Secchi disc depth.

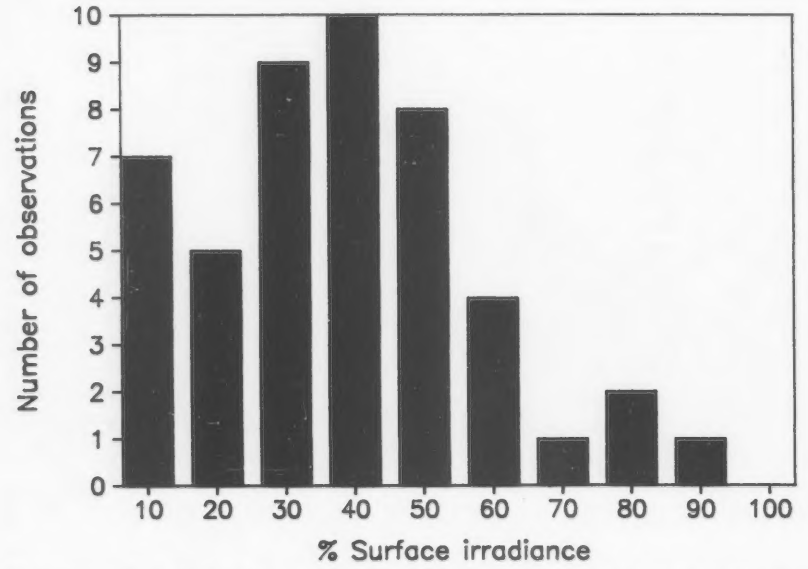

FIG. 5. Frequency distribution of the percent surface irradiance reaching the depth where the maximum submerged biomass occurs (Z_b).

Z_c and the latitude and transparency of the lakes. Indeed linear regression shows that 37% of the variation in the irradiance received at Z_c can be explained by considering the transparency and latitude of the lakes. Therefore, plants in tropical lakes appear to be able to grow where the surface irradiance is lower, relative to the surface values, than those in temperate lakes.

We then tested whether plants at lower latitudes are able to colonize deeper than at higher latitudes. The best equation to predict Z_c is

$$(3)\quad Z_c^{0.5} = 0.8 + 1.0S_D^{0.5} - 0.11S_D - 1.3 \times 10^{-4}\,\text{lat.}^2$$
$$r^2 = 0.58;\ N = 160;\ \text{SE}_{(\text{est.}^{0.5})} = 0.41;\ F_{S_D^{0.5}} = 134;$$
$$F_{S_D} = 45;\ F_{\text{lat.}^2} = 13.$$

These results support the idea that submerged plants grow deeper in warmer, better irradiated, tropical lakes than in temperate ones. However, water transparency accounts for

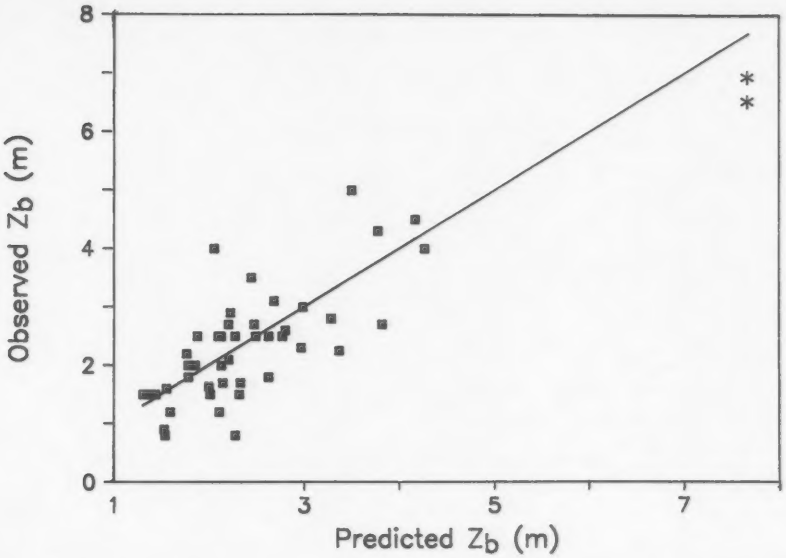

FIG. 6. Predicted versus observed depth of maximum biomass (Z_b) calculated from Eq. 4. The two astericks represent two extreme data points that were not included in the computation of the regression equation.

more variation than latitude. Additionally, Eq. 3 indicates that the relative increase in Z_c for a given increase in water transparency is lower for clear water lakes.

Depth of Maximum Biomass

The relationship between water transparency and Z_b is weak ($r^2 = 0.25$, Fig. 4), and similar in precision to that obtained by Chambers and Kalff (1985). This suggests that the extinction of light in the water per se has little influence on Z_b. Further evidence for this interpretation is obtained from an examination of the distribution of the percent surface irradiance received at Z_b (Fig. 5). This shows that, unlike Z_c (Fig.3), maximum growth of submerged plants occurs over a much wider range of percent surface irradiances.

The extent to which the plants use the space above them for growth is probably influenced by the length of the growing season, the incoming irradiance, and the temperature. Since all these factors are functions of latitude, we tested whether latitude explains the large variation in Z_b at a particular transparency in a multiple regression. The resulting equation is

$$(4)\quad Z_{mb}(\text{m}) = 1.09 - 0.02S_D{}^2 + 19.5(S_D/\text{lat.})$$
$$r^2 = 0.52,\ N = 45,\ \text{SE}_{\text{est.}} = 0.67;\ F_{S_D{}^2} = 4.5;\ F_{S_D/\text{lat.}} = 42$$

where the two lakes with the highest Z_b (Fig. 6) were not included in the calculation so as not to influence the relationship (Eq. 4) by two extreme points; however, including these values does not change the coefficients significantly ($P > 0.25$), but the r^2 increases to 0.75. Equation 4 indicates that the depth of maximum biomass increases with decreasing latitude. It also suggests that at a given latitude the increase in Z_b as transparency increases is lower in clear lakes. Unlike the case for the depth of maximum colonization, latitude explained a larger fraction of the variance in Z_b than water transparency.

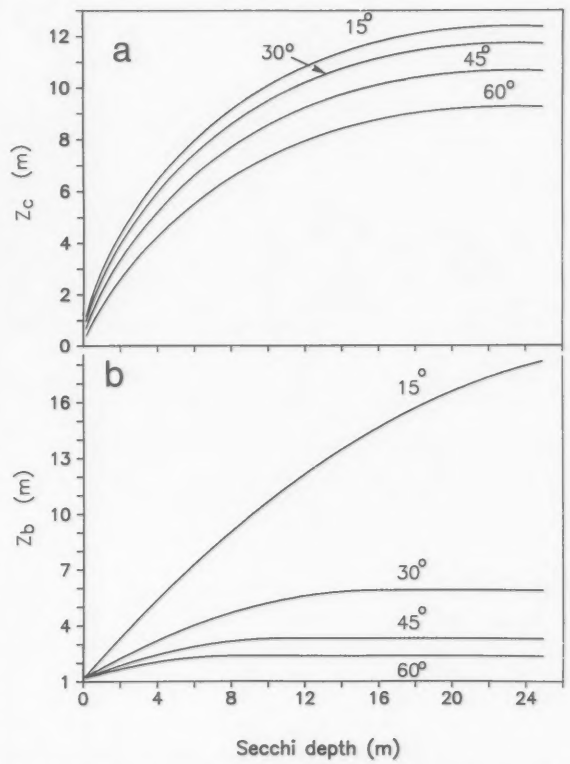

FIG. 7. Predicted changes in (a) the depth of maximum colonization Z_c and (b) the depth where the maximum biomass (Z_b) occurs as a function of the Secchi disc and latitude.

Discussion

The climatic differences associated with lake latitude appear to have a strong influence on the relationship between the depth distribution of submerged plants and the water transparency. At low latitudes, angiosperms colonize deeper and reach maximum biomass at greater depths than those growing in lakes of similar transparency at higher latitudes. Whether these relationships result from the warmer temperature, greater incoming irradiance, or longer growing season in low-latitude lakes cannot be resolved here. There is some evidence for the effect of all three variables. Increased irradiance and temperature increase photosynthesis of submerged macrophytes (Ikusima 1965), and these two factors interact to enhance the growth and biomass of submerged plants (Barko and Smart 1981; Barko et al. 1982).

Macrophyte biomass increased following thermal pollution of Lakes Wabamum (Haag and Gorham 1977), Stechlin (Krausch 1985) and Par Pond (Grace and Tilly 1976). Unfortunately, the light climate of these lakes is not reported, so the evidence is circumstantial. The effects of longer growing seasons are likely to compound the effects of higher temperature and irradiance. The variation in Z_b and Z_c left unexplained by latitude and water transparency is not very large relative to their variation within individual lakes; however, it suggests that other factors, such as the spectral composition of the underwater light field (Spence 1976) or interspecific variations in light compensation points (Canfield et al. 1985), may also influence Z_c and Z_b.

Although irradiance and temperature probably interact in the observed effect of latitude, the models (Eq. 3 and 4) suggest what their relative importance may be. The model for Z_c (Eq. 3) indicates that the depth of colonization is probably more influenced by water transparency than by latitude (Fig. 7a). This suggests that latitude acts through its influence on light levels in the determination of the maximum depth of colonization, because the Beer–Lambert law predicts linear changes in underwater irradiance with changes in surface irradiance (i.e. those due to latitude) and exponential changes with changes in extinction coefficient (i.e. changes in Secchi depth). In contrast, the overwhelming importance of latitude on Z_b (Fig. 7b) suggests that Z_b is more affected by temperature or length of the growing season than by the change in irradiance with latitude.

Similar changes in Secchi depth affect the depth distribution of submerged plants differently depending on latitude (Fig.7). The greater Z_c and Z_b for similar water transparencies in low-latitude lakes (Fig. 7) indicate that submerged macrophytes should play an increasingly important role at lower latitudes. Management designed to increase water transparency may be counterproductive in subtropical and tropical lakes, as increased transparency will markedly increase macrophyte abundance.

Acknowledgements

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NOTES

Calcium and Taurine Interaction in the Heart of the Crab *Carcinus maenas*

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Zatta, P. 1987. Calcium and taurine interaction in the heart of the crab *Carcinus maenas*. Can. J. Fish. Aquat. Sci. 44: 1765–1768.

Calcium and taurine were analyzed from the neurogenic heart and other tissues of *Carcinus maenas*. The interaction between calcium and taurine was studied in vitro using a potentiometric method. The hypothesis that calcium can modulate flux through the cell membrane as in the mammalian heart as a consequence of a taurine–calcium complex formation is untenable for the heart of *C. maenas*.

On a analysé les teneurs en calcium et en taurine présentes dans le coeur neurogène et les autres tissus de *Carcinus maenas*. On a étudié l'interaction *in vitro* entre le calcim et la taurine à l'aide d'une méthode potentiométrique. L'hypothèse selon laquelle le calcium peut moduler le flux à travers une membrane cellulaire, comme chez le coeur d'un mammifère, suite à la formation d'un complexe taurine–calcium est insoutenable dans le cas du coeur de *C. maenas*.

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Taurine, 2-aminoethansulfonic acid (NH_2–CH_2–CH_2-SO_3H), is a chemically stable amino acid analogue of β-alanine. It is widely distributed in animals, and also occurs to a limited extent in plants. Taurine was identified for the first time in ox bile by Tiedeman and Gmelin (1827) and considered as simply an excretory product. Later, taurine was found in the tissues of invertebrates (Valenciennes and Fremy 1855) and has now been found in practically all animal species examined (Awapara 1962).

Kossel and Edlbacher (1915) first hypothesized a physiological role of taurine as an osmolyte, and this has been confirmed by many workers, especially in the last two decades. In invertebrates, taurine can play at least three major roles: (a) as an osmotic effector (Gilles 1983); (b) as a participant in transphosphorylation processes (Allen and Garrett 1971); (c) as a chemical messenger in the nervous system (Dudel et al. 1963).

As much as 50% of the free amino acid content of mammalian heart consists of taurine (Jacobsen and Smith 1968). Tissues of marine organisms, especially invertebrates, possess concentrations of taurine, even higher than those found in tissues of mammals (Gregory and Robbin 1960).

Some authors (Dolara et al. 1979) demonstrated that taurine has a positive inotropic effect on the heart of vertebrates and modifies the intracellular calcium level. Decreasing contractile strength following heart perfusion without calcium can be counterbalanced with taurine in the medium (Dolara et al. 1979). This experiment demonstrates that taurine can modify the kinetic flux of calcium, reducing a calcium loss from the cardiac fibers, thus permitting higher calcium availability. This suggests that the action of taurine can be calcium dependent.

It has also been hypothesized that taurine can modulate the rate of calcium efflux in the heart. This observation, underlining the role of taurine as an osmoregulator, may indicate a possible correlation and/or interaction with calcium. Experiments reported in the literature indicate that taurine exerts a marked effect on calcium distribution in the heart of vertebrates (Dolara et al. 1973). With the aim to better understand the role of taurine and its possible relationship with calcium, I studied the interaction between calcium and taurine in the heart of the crab *Carcinus maenas*. I reject the hypothesis that formation of the calcium–taurine complex is an explanation for calcium flux regulation in the heart of *C. maenas*.

Materials and Methods

Analysis of free amino acids in the tissues of *C. maenas* was carried out after tissue extraction with 70% ethanol following the method of Evans (1972).

The calcium–taurine stability constant was determined by the potentiometric method, which consists of a titration cell of 50 mL, with a glass and a reference electrode connected to a millivoltmeter. In the titration cell, containing solutions with different concentrations of metal/ligand and in the presence of 0.5*M* NaCl, titration was carried using 0.1 *M* NaOH (see also Magon et al. 1972).

Uptake of taurine was measured using [^{14}C]taurine (Amersham). All measurements were carried out in aqueous solution at 20°C in 0.5 *M* NaCl. Before scintillation counting, tissues were digested in concentrated HNO_3 (Suprapur Merck).

Artificial seawater was prepared with the following composi-

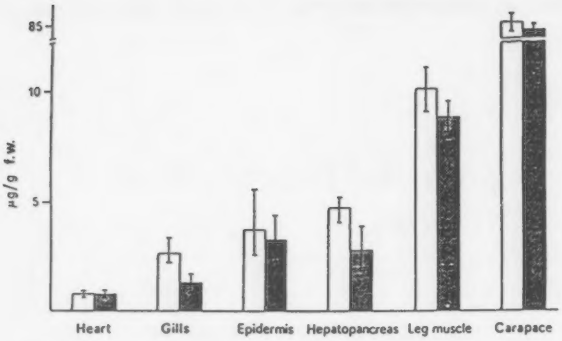

FIG. 1. Calcium content in the different tissues and organs of *C. maenas* after acclimation in artificial seawater at 15°C for 5 h with (open) and without (shaded) calcium in the medium. Bars represent $\bar{X}$ ± SEM. The experiment was carried out with 10 animals and each crab was kept in a small well-areated aquarium. The experiment was repeated three times for a total of 60 crabs.

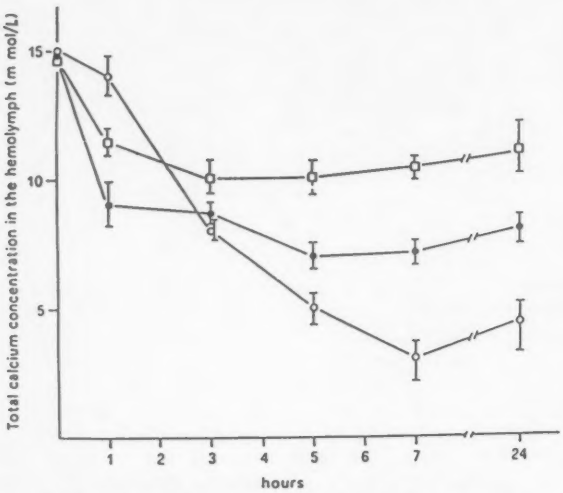

FIG. 2. Calcium concentration in the hemolymph of *C. maenas* kept in well-aerated small aquaria at 15°C. Groups of three animals for each experimental time (1, 3, 5, 7, and 24 h) were kept in three different calcium concentrations: 10 mmol/L (○), 2.5 mmol/L (●), and 1.25 mmol/L (□). Bars represent $\bar{X}$ ± SEM. Experiments were repeated four times for a total of 180 crabs.

tion: NaCl, 30 g/L; KCl, 0.38 g/L; $NaHCO_3$, 0.20 g/L; K_3PO_4, 0.1 g/L; Mg_2SO_4, 2.6 mg/L; $CaCl_2$, 40 mg/L or the quantity specified in the different experiments.

Calcium analysis was carried out using an atomic absorption spectrophotometer (Perkin Elmer 4.000). Tissues were previously digested in concentrated HNO_3 at 55°C.

Explant hearts were used immediately after removal from living animals previously anesthetized in ice. Animals were kept in well-aerated aquaria and fed twice weekly with clams. Experiments were carried out at 15°C 2 d after feeding and replicated as reported in the figure legends.

Results

In normal seawater at 15°C the concentration of calcium in the different tissues varies from 0.8 µg/g fresh weight (f.w.) in the heart to around 10 µg/g f.w. in the leg muscle (Fig.1). The highest concentration was observed in the carapace which is equal to 85 µg/g wet weight. After 5 h in artificial seawater without calcium when animals give signs of suffering such as low mobility, disorientation, low response to external simulation, etc., the concentrations of calcium were quite different. There was a 50% decrease in calcium in the hepatopancreas and in the gills, an 11% decrease in the epidermis, 17% in the leg muscle, and 3% in the carapace. The lowest decrease observed was in the heart (0.5–0.8%).

When animals were transferred into an environment with a lowered calcium concentration, the calcium of the hemolymph decreased rapidly, but after 5–7 h there was a partial recovery (Fig.2). Animals do not survive more than 10 h in calcium-free seawater. Experiments were carried out on 15 animals kept in single well-aerated aquaria at 15°C and the experiment (three for each experimental time and in three calcium concentrations) was repeated three times. Variations in calcium of the external environment produce changes in the free amino acid pool of the heart (Fig.3). When calcium concentration decreased, taurine concentration decreased significantly. Other amino acids are generally inversely related to calcium concentration. In fact, glutamic acid, glycine, alanine, and arginine increase significantly with decreasing calcium concentrations in the external medium. In animals transferred from normal seawater containing 400 mg Ca/L to a medium containing 100 mg Ca/L, aspartic increased 5 times, glycine 2 times, alanine 1.5 times,

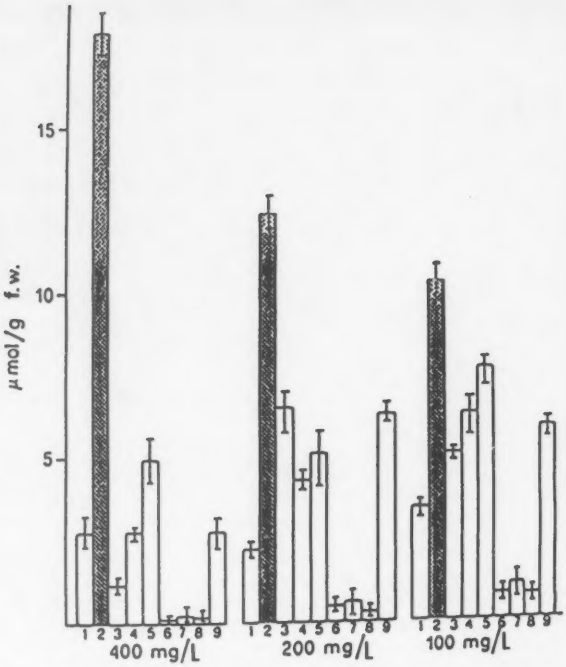

FIG. 3. Free amino acid concentration from hearts of *C. maenas*. Each of three groups of animals was kept at 15°C in three different calcium concentrations (400, 200, and 100 mg/L). Bars represent $\bar{X}$ ± SEM. Animals were maintained in individual aquaria and the experiments were repeated three times for a total of 90 crabs. 1, Phosphorylethanolamine; 2, taurine; 3, glutamic acid; 4, glycine; 5, alanine; 6, leucine; 7, lysine; 8, histidine; 9, arginine.

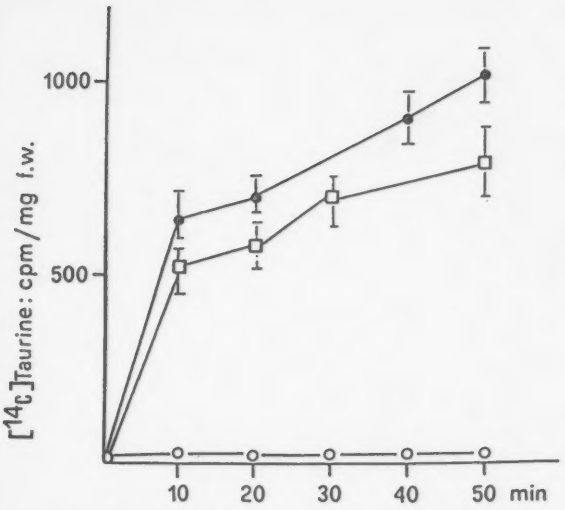

FIG. 4. Uptake in vivo of [^{14}C] taurine in the heart of 10 animals, in individual aquaria for each experimental condition, as a function of time. ○, 0 mg/L; □, 100 mg/L; ●, 400 mg/L. Bars represent $\bar{X}$ ± SEM. Experiments were repeated three times for a total of 90 crabs.

and arginine about 2 times. Taurine decreased about 1.6 times, but being 50% of the total free amino acid pool, it represents in any case the highest contribution to cell volume regulation. Amino acid analyses were carried out in animals kept in single aquaria (three groups of 10, each group in a different calcium concentration) and each experiment was repeated three times for a total of 30 crabs. No uptake of [^{14}C]taurine was observed upon incubation of the heart of *C. maenas* in free calcium artificial seawater (Fig.4), but an increase in taurine uptake was observed when calcium concentration was increased in the medium.

The stability constant of the calcium–taurine complex was determined potentiometrically in the presence of 0.5 *M* NaCl, i.e. close to the normal physiological condition of *C. maenas*. A value of log $\beta_{ML} = 0.7$ was determined, which is comparable with data obtained by Irving et al. (1982) using a ^{13}C chemical shift titration curve of the calcium–taurine system.

Discussion

When *C.maenas* is transferred into an environment without calcium, animals cannot survive. They give signs of suffering within a few hours and die after no more than 10 h. In this kind of stressed situation, calcium can be mobilized from different tissues in different ways. In the absence of environmental calcium the calcium concentration in the tissues is reduced from about 10 to 50%; the only exception seems to be the heart where only a very small quantity of calcium is lost (about 0.8% of the total initial value). Activation of the calcium transport mechanism is fundamental in the regulation of calcium in the hemolymph of *C. maenas* (Greenway 1976). In my data, calcium in the hemolymph has a concentration of 15 mmol/L, which is comparable with that reported by Greenway (1985), and when animals are transferred into an environment with low calcium concentration, they always remain hyperionic with respect to the external calcium concentration (Fig.2). Greenway (1976) reported that active regulation of calcium appears to be stimulated by a fall in salinity rather than a change in calcium concentration in the medium. My data do not completely agree with this observation. In artificial seawater with a low calcium concentration, *C. maenas* not only remains hyperionic with respect to calcium, but after 5–7 h of acclimation it begins slowly to recover showing a possible active uptake. It has also been reported that in vertebrates, the contractility of the heart of guinea pig and rat is reduced when perfused with low-calcium medium (0.14 m*M*) (Grosso and Bressler 1976). In the Arthropoda, calcium has an antagonistic action with respect to monovalent cations such as potassium on the activity of the cardiac pacemaker. An excess of calcium inhibits the pacemaker and the heart stops in diastole. Deficiency of calcium in the Arthropoda can accelerate the cardiac frequency, and without calcium the heart stops in sistole (Capraro 1968). In addition, a change in calcium can modify the concentration of the free amino acid pool in the heart (Fig.3). The effect is particularly evident in the case of taurine which decreases dramatically reducing calcium concentration in the external medium; on the contrary, other amino acids such as glutamic acid, glycine, alanine, and arginine increase. Total free amino acid concentration excluding taurine increases when the calcium concentration of the external medium is reduced. Taurine is present in high concentration in the heart, where it constitutes 50% or more of the free amino acid pool (Fig.3).

Dolara et al. (1979), studying the calcium–taurine formation constant, calculated that about 8% of the total calcium present in the mammalian myocardium exists as a taurine complex. However, some authors (Irving et al. 1982) have observed that there is difficulty in reaching a precise determination, in measurements using the natural abundance of ^{13}C in chemical shift titration curves, which could have led to an incorrect conclusion.

The hypothesis that taurine can modulate the calcium flux in the heart by forming a complex with calcium is of particular interest, not only in terms of the physiology of the heart but also in terms of understanding of the high concentration of taurine in this organ. It has been hypothesized that taurine increases the affinity of some cell structures for calcium (Dolara et al. 1973). In the heart of *C. maenas*, in the absence of calcium there is no taurine uptake, while an increase in taurine uptake occurs following an increase of calcium concentration in the external medium.

In other experiments with myocardial cells (Irving et al. 1982) in which the concentration of taurine was equal to 39 m*M*, only 14% of calcium available for complexation was bound to taurine. The capability of taurine to influence calcium flux and vice versa by direct complexation to calcium depends on the portion of free intracellular calcium which can be mobilized by taurine.

It has also been reported that taurine can reduce the rate of calcium efflux from the exchangeable pool, thus increasing the total sequestring capacity. Taurine may also function as a membrane stabilizer (Huxtable and Bressler 1973).

Data reported here do not seem to justify the conclusion of a taurine flux in the heart of *C. maenas* as a consequence of a calcium–taurine complex formation. In fact, the value of constant formation reported here predicts that only a negligible amount of calcium is bound to taurine. This is coherent with previous data concerning the high instability of calcium–taurine complexes in comparison with other metal–taurine complexes (Greenstein and Winitz 1961).

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Effects of Nutrient Pulses on Community Structure and Cell Size of a Freshwater Phytoplankton Assemblage in Culture

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A natural assemblage of phytoplankton was removed from an oligotrophic lake and grown in semicontinuous culture under three nutrient addition frequencies, ranging from one addition every 4 d to one addition every 16 d. Changes in community structure, cell size, and nutrient chemistry were determined at several times during the 35-d experiment. Under the least frequent nutrient addition regime, cultures were dominated by *Tabellaria fenestrata*; in contrast, when nutrients were added more often, *Synedra radians* was dominant. As well as causing a shift in species composition, under the once per 16 d nutrient addition frequency the average cell volume increased from approximately 500 to 1300 μm^3. This was mainly the result of the larger size of *T. fenestrata*, but was also in part because of an increase in the cell size of *S.*

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radians. It is argued that cells which are able to sustain elevated maximum uptake rates, and which are able to store the largest amount of nutrient relative to their minimum requirements, should be successful under conditions where saturating pulses of limiting nutrients occur.

On a prélevé un assemblage naturel de phytoplancton d'un lac oligotrophe pour le garder en culture semi-continue à trois différentes fréquences d'apports de matières nutritives allant d'un apport tous les quatre jours à un apport tous les seize jours. Plusieurs fois pendant l'expérience, d'une durée de 35 j, on a déterminé les variations de la structure de la communauté, de la taille des cellules et des paramètres chimiques des matières nutritives. Au régime d'apports alimentaires les moins fréquents, les cultures étaient dominées par *Tabellaria fenestrata*; par contre, aux apports plus fréquents, *Synedra radians* était l'espèce dominante. En plus de modifier la composition spécifique, les apports tous les 16 j ont eu pour effet de faire augmenter le volume cellulaire moyen d'environ 500 à 1300 μm^3. Cela résulte de la plus grande taille de *T. fenestrata* et, dans une moindre mesure, d'une augmentation de la taille des cellules de *S. radians*. On formule l'hypothèse que les cellules qui sont capables de maintenir des taux de captation maximum élevés et d'emmagasiner de grandes quantités de bioéléments par rapport à leurs besoins minimums devraient prospérer dans des conditions où il existe des phases intermittentes de saturation de bioéléments limitatifs.

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Aquatic ecologists have puzzled for years as to why so many species of phytoplankton are able to coexist in an apparently homogeneous environment (e.g. Hutchinson 1961). Typically, one can observe literally tens of phytoplankton species in a thimble-full of water taken from any number of aquatic habitats. Over the years it has become apparent that many processes are occurring which in concert probably explain the enormous diversity that we observe in phytoplankton communities. A partial list of these processes would include selective predation by zooplankton (Ganf 1983), bacteria (Burnham et al. 1984),viruses (Mayer and Taylor 1979), and fungi (Gaertner 1979), allelopathy (Keating 1977), differential mortality in predator digestive tracts (Porter 1975; Johnson et al. 1982), differential sinking rates (Walsby and Reynolds 1980; Harrison et al. 1986), changes in light quantity and quality (Wall and Briand 1979), utilization of alternative sources of the same nutrient (Antia et al. 1980), auxotrophic requirements (Bonin et al. 1981), facultative phagotrophy (Daley et al. 1973; Bird and Kalff 1986), inherent spatial and temporal variability in aquatic environments (Richerson et al. 1970), ability of some phytoplankton to produce metal-binding substances (Murphy et al. 1976), and limitation of different species by different resources (Tilman 1977; Kilham 1986).

Empirical evidence indicates that resource fluctuations may also be an important factor affecting phytoplankton community structure. Studies have shown that the frequency of nutrient addition can affect species richness (Robinson and Sandgren 1983; Sommer 1985), competitive outcome (Turpin and Harrison 1979; Scavia et al. 1984; Sakshaug and Olsen 1986), and cell size (Turpin and Harrison 1980). In nature, limiting resources are thought to be injected into nutrient-deficient surface waters by a variety of mechanisms, ranging in scale from the excretion "plumes" of individual zooplankton to major mixing events caused by upwelling or storm activity. However, the understanding of how such events may affect phytoplankton assemblages is still very limited.

The primary purpose of this study was to examine the influence that large-scale nutrient pulsing has on freshwater phytoplankton community structure and cell size.

TABLE 1. Concentrations ($\mu g \cdot L^{-1}$) of nutrients in the water collected from Great Central Lake.

Total P	4
Total dissolved P	1
Soluble reactive P	<1
Silicate	2460
Nitrate + nitrite	36
Ammonium	4
Dissolved organic N	50

Materials and Methods

Culturing — Water was collected in February 1980 from Great Central Lake, a moderately large (55km^2) oligotrophic lake on Vancouver Island in southwestern British Columbia, Canada (49°22′N, 125°15′W). Limnological details are provided in LeBrasseur et al. (1978) and Stockner et al. (1980). Two hundred litres of water was collected from the 1-m depth and immediately filtered through 120-μm screening to remove large grazers. Temperature at the time of collection was 3.6°C; nutrient concentrations are shown in Table 1. Twenty litres of this water was placed in a polyethylene carboy in an incubator under continuous irradiance; over the next 6 d the temperature was gradually increased to 10°C and the irradiance from 25 to 120$\mu E \cdot m^{-2} \cdot s^{-1}$. The remaining 180 L of water was filtered through 0.45-μm nitrocellulose filters and stored in the dark at 4°C.

Cultures were initiated with 1 L of 120-μm-filtered lake water and 1 L of 0.45-μm-filtered lake water added to each of eight 2.8-L borosilicate Fernbach flasks. The positions of the flasks in the incubator were initially randomly assigned and then switched when diluted to minimize any possible light effects. Every 2 d the cultures were thoroughly mixed and diluted by pouring off 1 L of culture and replacing it with the same volume of 10°C, 0.45-μm-filtered lake water. This results in a dilution rate (D) of $0.35 \cdot d^{-1}$ ($D = (-\ln f)/2$ where f is the fraction of original volume remaining subsequent to a dilution). Each

culture was supplied with additional N and P either once per 4 d, once per 8 d, or once per 16 d, with all treatments beginning on day 3 of the experiment. Pulses were administered by supplementing the filtered lake water with ammonium nitrate and ammonium phosphate at an N:P ratio of 15:1 (by atoms). Concentrations of the pulses were varied such that each culture received the same nutrient flux over 16 d (40.2 μg of $P\text{-}PO_4^{3-}$, 117.6 μg of $N\text{-}NO_3^-$, and 154.0 μg of $N\text{-}NH_4^+$). As well, all cultures received significant additional quantities of dissolved inorganic N from the regular once per 2 d dilution with filtered lake water. The concentration of soluble reactive P (SRP) in the filtered lake water was below the detection limit (Table 1). The resulting N:P supply ratio (by atoms) to the cultures was between 27:1 and 33:1 and the Si:P supply ratio was between 895:1 and 1086:1, assuming PO_4^{3-} concentrations of 1.0 and 0.00 $\mu g \cdot L^{-1}$, respectively, in the filtered lake water.

Phytoplankton and nutrient analyses — Samples were enumerated for species composition and cell size on five occasions during the experiment. Cell numbers were estimated by counting a minimum of 200 cells of each species, except where species were so rare as to make this impractical. Counts were made on 10-mL settled samples, under 400× magnification (Lund et al. 1958). Cell or frustule (for diatoms) volumes were calculated for a minimum of 35 cells of each species, for each sampling date, using formulae for similar geometric shapes. Samples were taken at the beginning and end of the experiment and prior to pulsing events (days 11 and 19). As well, samples were taken on day 25, between pulsing events. The contribution of certain species to the total cell volume of algal cultures has been observed to oscillate with the frequency with which a culture is pulsed with nutrients. However, such oscillations tend to be in phase with the frequency of resource addition (Sommer 1985), and hence, the species composition of samples taken at the same time with respect to a nutrient pulse is relatively stable.

Samples for nutrients were taken each time immediately prior to when the cultures were diluted. SRP was analyzed by the chemical technique of Murphy and Riley (1962), as outlined in Stainton et al. (1977). Analysis for ammonium (NH_4^+) was by the Solorzano (1969) technique, for nitrate (NO_3^-) by the method of Morris and Riley (1963), for total P and total dissolved P by the method of Traversy (1971), and for silicate (SiO_4^{4-}) as proposed by Armstrong (1951); these techniques were automated in the manner described in Stephens and Brandstaetter (1983). Dissolved organic N was analyzed as in Stephens and Brandstaetter (1983). Concentrations are expressed as micrograms of N, P, or Si per litre.

Results

Changes in the concentrations of SRP, NH_4^+, NO_3^-, and SiO_4^{4-} oscillated with the nutrient pulsing frequency (Fig. 1, 2, and 3). Under the two most frequent nutrient addition regimes the concentrations of these nutrients were low by the end of the experiment (Fig. 1 and 2); however, the relatively high N:P and Si:P supply ratios and the rapid depletion of added PO_4^{3-} suggest that P was limiting phytoplankton growth.

The replacement of *Rhizosolenia* sp. by *Synedra radians* was characteristic of the initial stages of all three treatments when expressed either as a proportion of total cell volume (Fig. 4) or as a proportion of total cell number (data not shown). *Synedra radians* remained dominant under the more frequently pulsed regimes, while *Tabellaria fenestrata* became co-dominant under conditions where nutrients were added least often.

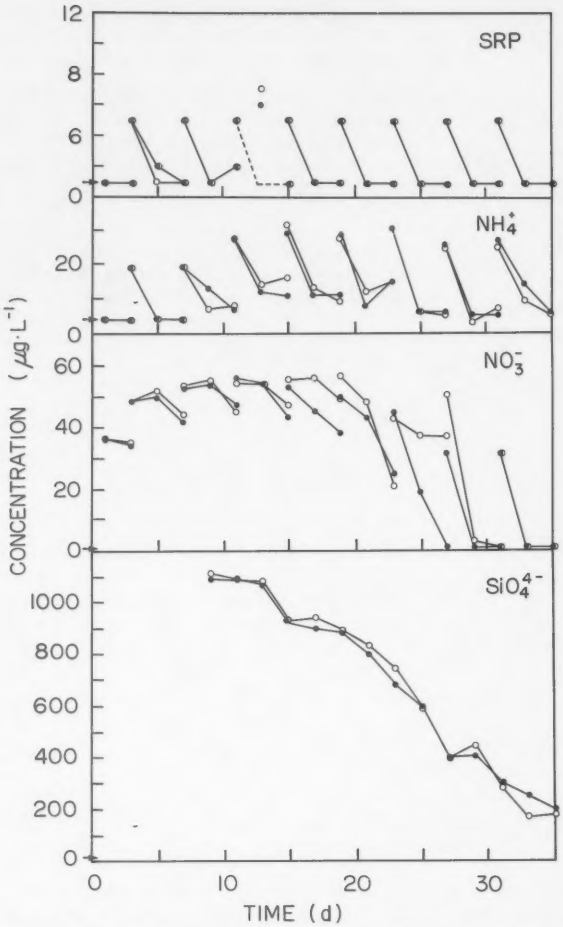

FIG. 1. Changes in the concentrations of P as soluble reactive P (SRP), N as ammonium (NH_4^+) and nitrate + nitrite (NO_3^-), and Si as reactive silicate (SiO_4^{4-}) in cultures to which nutrients were added every 4 d. Solid symbols = replicate I; open symbol = replicate II. Points are for single determinations. Broken lines indicate an assumed relationship when the occasional intervening value was unrealistic. Arrows indicate the detection limit for each nutrient. Where data points fall on each other, replicate II values have been offset slightly to the right.

The pulsing frequency also affected the phytoplankton size distribution; larger cells occurred when nutrients were added every 16 d (Fig. 5). This was mainly because of the much larger size of *T. fenestrata* (3466 μm^3, SD = 820, $n = 55$) relative to *S. radians* (880 μm^3, SD = 288, $n = 71$). However, it was also in part the result of a significant ($p < 0.001$, Mann–Whitney U test) increase in the length distribution (diameter was constant) of *S. radians* (Fig. 6). When nutrients were added most frequently, 37 and 39% of the cells were greater than 69 μm in length for replicates I and II, respectively. In contrast, under the least frequent nutrient addition regime, 81 and 75% of *S. radians* were longer than 69 μm for the two replicates, respectively.

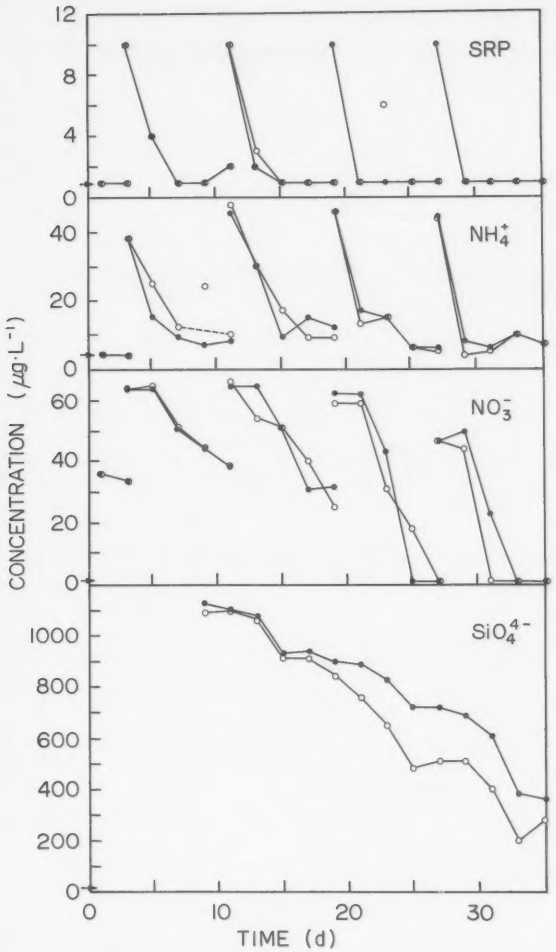

FIG. 2. As for Fig. 1; data are for cultures to which nutrients were added every 8 d.

Discussion

Community structure — The greater importance of *Tabellaria* when nutrients were added least often was apparently the result of the nutrient addition regime and was not attributable to different relative resource requirements (sensu Peterson 1975; Tilman 1977). The N:P and Si:P supply ratios to the cultures were in the range where diatoms would be expected to be P limited (Tilman 1982). Previous workers have shown that the genus *Synedra* is almost invariably the best P competitor at temperatures less than 18°C when nutrients are added continuously (Sommer 1983, 1985; Smith and Kalff 1983; Tilman and Kiesling 1984; Kilham 1986), or even when pulsed at weekly intervals (Sommer 1984, 1985). In our study, *Tabellaria* only came into prominence when additional nutrients were administered at 16-d intervals. Under this treatment, concentrations of NO_3^- and SiO_4^{4-} remained high while SRP remained below detection. Such conditions would be expected to favour dominance by *Synedra*.

In addition to theoretical arguments (Grenney et al. 1973; Tilman et al. 1982), empirical data have also shown that the frequency of addition of a limiting resource can affect the outcome of competition in phytoplankton cultures. Using N-limited chemostats initiated with natural assemblages of marine phytoplankton, Turpin and Harrison (1979, 1980) found

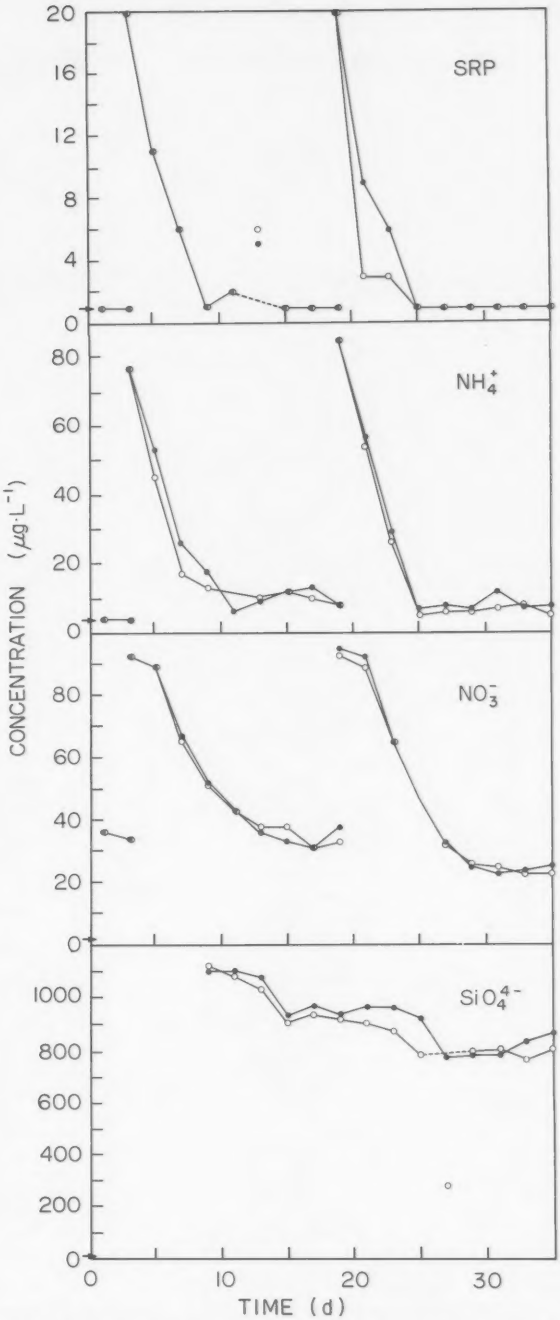

FIG. 3. As for Fig. 1; data are for cultures to which nutrients were added every 16 d.

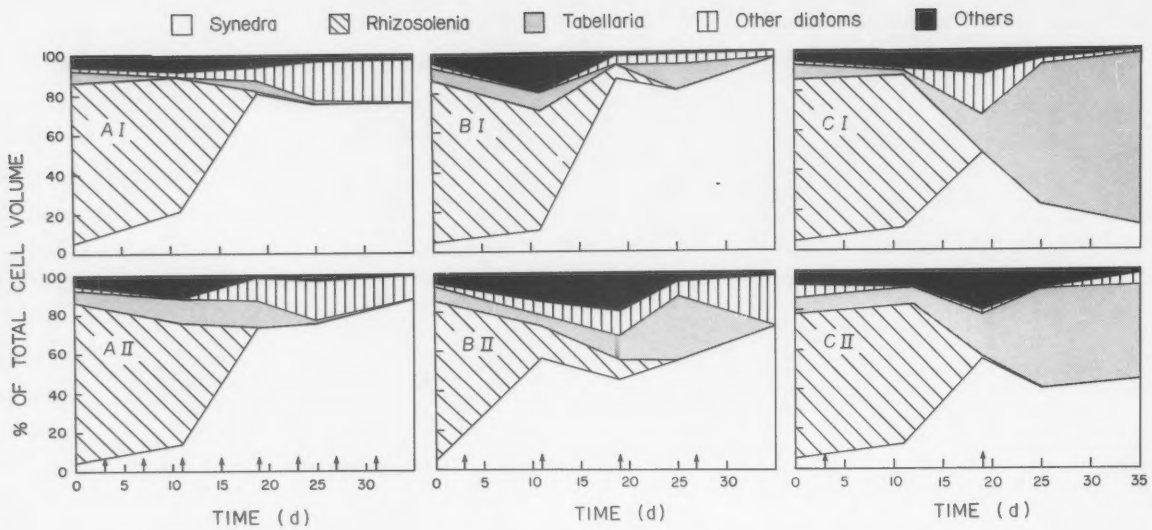

FIG. 4. Proportion of total phytoplankton cell volume made up by each cell type for each replicate (I and II). Nutrients were added (A) once every 4 d, (B) once every 8 d, and (C) once every 16 d. Arrows indicate time of nutrient additions.

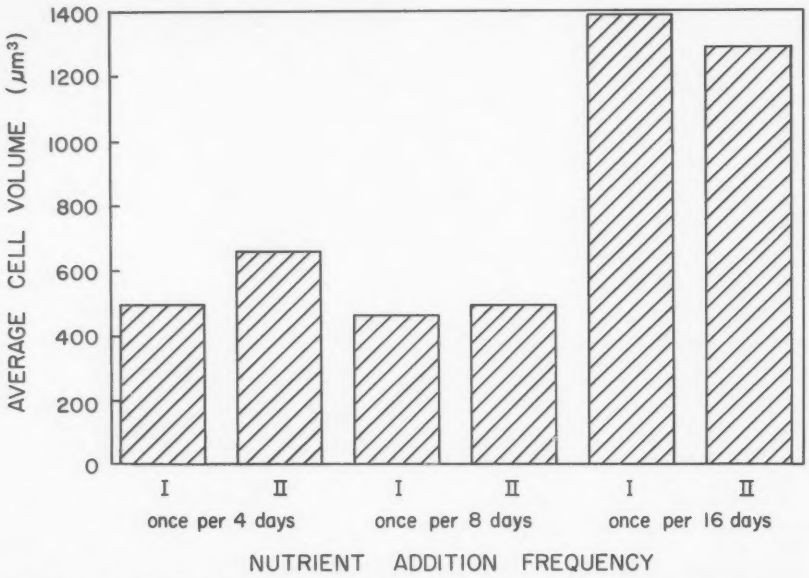

FIG. 5. Average cell volume as a function of nutrient addition frequency for replicate cultures (I and II) at the end of the experiment.

that competitive dominance could be shifted between different diatom genera, depending on the schedule of NH_4^+ addition. As well, Scavia et al. (1984) and Sakshaug and Olsen (1986) were able to demonstrate that short-term nutrient patchiness can affect competitive outcome in P-limited freshwater phytoplankton cultures. Our results extend these findings to demonstrate that patchiness on the scale of weeks is potentially an important process influencing community structure and that the presence of *T. fenestrata* in P-limited field populations may be indicative of infrequent pulses of PO_4^{3-} into the epilimnion. Results of Stockner and Shortreed (1975) showing *T. fenestrata* to be associated with periodic upwelling events would seem to support this hypothesis.

Cell size — We also observed an increase in cell volume under conditions where nutrients were added least often. Similar results were reported by Turpin and Harrison (1980) who found that decreases in the frequency of nutrient additions from continuous to once weekly resulted in larger cells, although their observations were made on NH_4^+-limited cul-

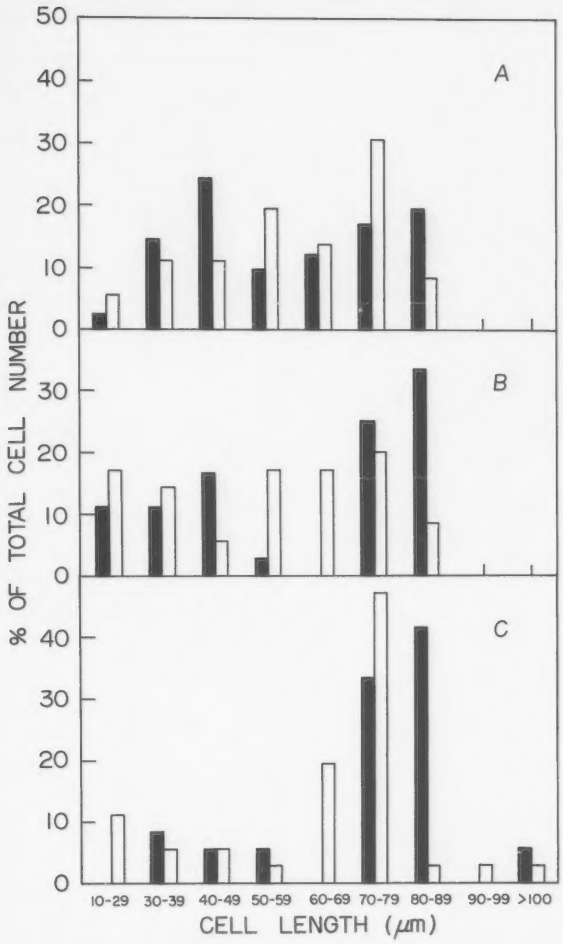

FIG. 6. Frequency distributions of cell length for *S. radians* as a function of nutrient addition frequency at the end of the experiment. Culture designation (A, B, and C) as in Fig. 4; shaded = replicate I; open = replicate II.

tures of marine phytoplankton. In contrast, we did not observe changes in cell size in response to pulsing frequencies of less than 2 wk. As well, we believe that our observation that the cell size of *S. radians* was larger under the least frequent nutrient addition scheme is the first report of a change in nutrient addition frequency resulting in a shift in the size distribution of a species.

The mechanism whereby nutrient pulsing frequency is able to affect cell size and community composition is unclear. It has been suggested by Turpin and Harrison (1980) that because smaller cells have a higher specific respiration rate, they may be less able to survive periods of nutrient deprivation. Therefore, they would be rarer when resource supplies were infrequent.

An alternative explanation that has been invoked to account for changes in community structure in response to nutrient fluctuations is that individual species possess uptake kinetics that specialize on different aspects of a fluctuating resource. Phytoplankton uptake kinetics are generally approximated by a rectangular hyperbola of the form

$$V = \frac{V_{max} \cdot S}{k_S + S}$$

where V is the uptake rate per cell, V_{max} is the maximum uptake rate, S is the resource concentration, and k_S is the resource concentration at which half the maximum uptake rate occurs. It is envisaged that species with a high V_{max} for the limiting resource can take advantate of nutrient pulses, while species with a low K_S are better able to accumulate the resource when the ambient concentration is low (Eppley et al. 1969; Turpin and Harrison 1979). In fact, it is the initial slope of the uptake curve (V_{max}/k_S) and not k_S per se which should dictate the ability to sequester the resource at low substrate concentrations (Healey 1980). As well, although the value of V_{max} has influence on competitive advantage , a more important factor when considering large nutrient pulses is the duration over which V_{max} is sustainable. Suttle and Harrison (1986) have shown that very large differences exist in the ability of P-limited species to maintain elevated PO_4^{3-} uptake rates, but that the capacity to sustain elevated uptake rates is not necessarily only associated with larger cells.

Related to the maximum uptake rate, and what dictates the success with which a species will capitalize on a saturating pulse of a limiting nutrient, is its ability to sequester the resource relative to its minimum requirement. Strictly speaking, the ratio of the maximum amount of nutrient that can be accumulated to the minimum amount required to maintain a positive net growth rate should be a good measure of the competitive ability of a species when nutrient patches are large. It is an indirect measure of the number of daughter cells which can be produced from a given nutrient patch assuming that the nutrients once stored are recoverable and that losses by excretion are negligible. Intuitively, bigger cells would be expected to have an advantage because of their potentially larger storage capacity; however, whether this is adequate to offset their larger minimum requirements (Shuter 1978) is not certain. Results from our experiments suggest that it is true for *T. fenestrata*.

It is also evident that species are able to alter their physiology in response to particular patchiness regimes. (Quarmby et al. 1982), and consequently, there is no a priori reason why a single species should not be a good competitor over a range of patchiness regimes. In fact, an increase in V_{max} without a concomitant increase in k_S would not only enable a species to sequester more nutrient during an elevated pulse, but would also increase its ability to sequester more nutrient at low ambient concentrations by virtue of the effect that an increase in V_{max} has on initial slope. Although NH_4^+-limited cultures of *Thalassiosira pseudonana* were not found to possess a steeper initial slope for uptake, despite an elevated V_{max} (Parslow et al. 1985), the possibility remains that some species may be capable of such a strategy. Perhaps this is why some species such as *Synedra acus* are able to dominate under P-limited conditions over a wide variety of nutrient addition regimes (Smith and Kalff 1983; Sommer 1983, 1984).

The results of these experiments indicate that resource patchiness on the scale of days to weeks can affect phytoplankton community structure in terms of cell size and species composition. Whether or not such patchiness has similar effects in the variable natural environment remains to be demonstrated.

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Fine-spotted Brown Trout (*Salmo trutta*): Its Phenotypic Description and Biochemical Genetic Variation

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Skaala, Ø., and K. E. Jørstad. 1987. Fine-spotted brown Trout (*Salmo trutta*): its phenotypic description and biochemical genetic variation. Can. J. Fish. Aquat. Sci. 44: 1775–1779.

Initial studies on a small population of brown trout (*Salmo trutta*) in the Hardangervidda area in Norway revealed specimens with remarkable morphological characteristics. About one third of the population was classified as "fine-spotted trout" due to the occurrence of small black spots on the body and fins. These individuals also have from four to seven black spots located around the pupil of the eye. Genetic data, obtained by electrophoresis of tissue enzymes, demonstrated large differences compared with other brown trout populations. According to the information available, the abundance of fine-spotted trout has decreased during the last eight decades, which focuses on the need for preservation of the population and its habitat.

Des études préliminaires portant sur une petite population de truites brunes (*Salmo trutta*) de la région de Hardangervidda (Norvège) ont révélé la présence de spécimens présentant des caractéristiques morphoqiques distinctes. Environ le tiers de la population a été classé comme « truites à petites taches », à cause de la présence de petites taches noires sur le corps et les nageoires. Ces individus présentaient aussi de quatre à sept taches noires autour de la pupille de l'oeil. Des données génétiques obtenues par électrophorèse d'enzymes somatiques ont révélé de grandes différences par rapport aux autres populations de truites brunes. Selon les données disponibles, l'abondance de truites à petites taches a baissé au cours des huit dernières décennies; on devra donc voir à la protection de cette population et de son habitat.

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Several salmonid fish species exhibit a great amount of variation in body colouration, meristic features, food preference, growth rate, growth potential, age at maturity, and behaviour. As previous authors have pointed out, the variation in such characters may be partly genetically and partly environmentally controlled (Alm 1948; Naevdal et al. 1978; Loudenslager and Kitchin 1979; Ferguson and Mason 1981; Carl and Healey 1984). Genetic variation is the basis for adaptability of natural populations, and is of fundamental importance for the continued evolution. In addition, genetic variation in natural populations serves as raw material for cultured populations. With no variation in heritable characters, there is no basis for genetic improvement, whether it concerns disease resistance in food plants or growth rate in farmed salmonids. From these facts it follows that genetic variation is a natural resource, and must be protected and monitored as such.

This note presents data on a Norwegan population of brown trout (*Salmo trutta*) where about one third of the individuals deviate considerably in body colouration from other Norwegian brown trout populations. The existence of different trout morphs within the lake may be explained by two alternative hypotheses. It may be a polymorphism in the spotting character within an interbreeding population, or alternatively, the two morphs represent two groups of trout that have differentiated allopatrically in a larger part of the genome, and have later come into contact. The purpose of this study was to describe the phenomenon and to look for genetic differences between the morphs in loci detectable by electrophoresis of tissue enzymes.

Materials and Methods

The population inhabits Lake Svartavasstjønn, a small lake in the upper reaches of a watercourse draining northern parts of the Hardangervidda area (Fig . 1). This lake, located about 1300 m above sea level, has an area of about 50 ha and a greatest recorded depth of 14 m. The potential spawning areas in outlets and inlets are limited.

In September 1985, 77 brown trout were sampled from Lake Svartavasstjønn by gill nets. One month later, 18 individuals were sampled from Lake Dragøyfjorden, 3 km downstream.

The length, weight, and sex of each individual were recorded. Scales were removed from 33 individuals from Lake Svartavasstjønn for estimation of age and growth rate. Each individual caught in the two lakes was assigned to one of the three categories "fine-spotted", "intermediate", and "large-

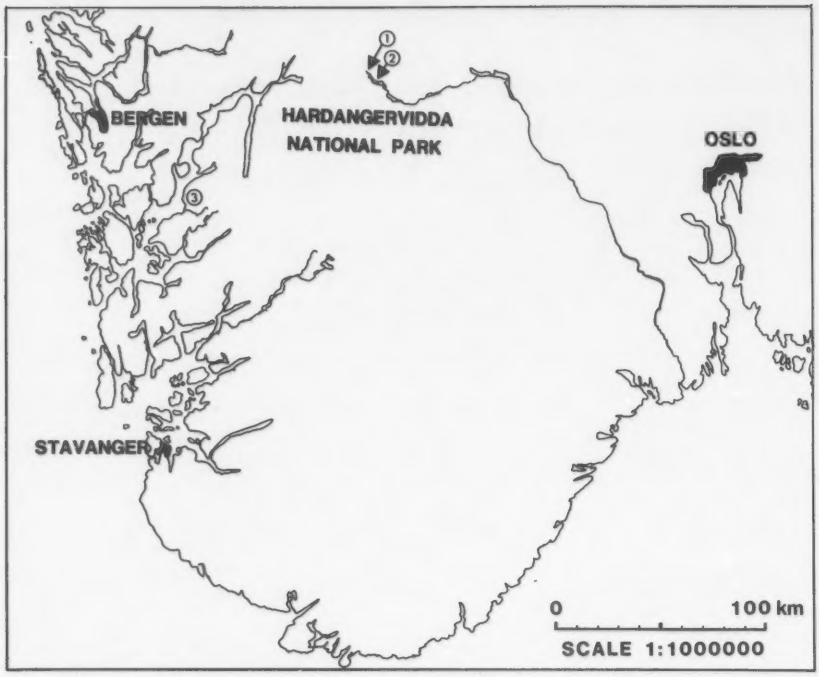

FIG. 1. Southwestern Norway. 1, Lake Svartavasstjønn; 2, Lake Dragøyfjord; 3, Lake Myrdalsvatn.

spotted" according to the size and pattern of black spots on the body and dorsal and caudal fins and in the eyes (Fig. 2).

Samples of muscle, liver, and eye tissue were taken for analyses of biochemical genetic variation. The tissue samples were immediately placed in liquid nitrogen where they were stored for about 2 wk until analysis by horizontal starch gel electrophoresis. Gels were made of 12% starch. Two buffer systems were used. (A) TCB gel buffer: 0.015 *M* Tris, 0.001 *M* citric acid, 0.003 *M* boric acid, and 0.001 *M* LiOH; electrode buffer: 0.3 *M* boric acid and 0.1 *M* LiOH; both buffers were adjusted to pH 8.6 (modified from Taggart et al. 1981). (B) AM gel buffer: 0.002 *M* citric acid; electrode buffer: 0.04 *M* citric acid; both buffers were adjusted to pH 6.1 with *N*-(3-aminopropyl)morpholine (modified from Clayton and Tretiak 1972).

The following enzymes were stained for: alcohol dehydrogenase, creatine phosphokinase, glucose phosphate dehydrogenase, lactate dehydrogenase, malate dehydrogenase, malic enzyme, phosphoglucose isomerase, and phosphoglucomutase, comprising 22 loci. Genetic loci were considered to be polymorphic if the freguency of the predominant allele was less than 0.99. Heterozygosity was estimated by calculating the expected heterozygote frequences from observed allele frequences. For genetic interpretation of the electrophoretic banding pattern, we follow the nomenclature proposed by Allendorf and Utter (1979). The genetic data were processed by using the BIOSYS-1 computer program of Swofford and Selander (1981).

Results and Discussion

Phenotypic Variation — The large-spotted morph found in Lake Svartavasstjønn was similar to common brown trout in nearby lakes and rivers (Fig. 2). The fine-spotted trout, on the other hand, was very distinct in having dense, fine black spots on the body and dorsal and caudal fins. The size of the fine spots was roughly one quarter the size of those found on common large-spotted brown trout. From four to seven (but normally four) black spots were located around the pupil of the eye. These spots were about one quarter the size of the pupil. The intermediate morph was rather similar to the large-spotted morph. It differed from the large-spotted morph, however, by having from one to four spots round the pupil of the eye. We have chosen the term "intermediate" for one of the morphs, as it is intermediate in appearance between the fine- and the large-spotted morphs. It must be emphasized, however, that so far we have no evidence that we are dealing with a genetic hybrid or a real cross between the fine-spotted and the large-spotted trout. The two most divergent morphs are shown in Fig. 3.

Except for Sømme (1954), who only mentioned the phenomenon very briefly, there is no written literature referring to this fine-spotted trout. The only population of brown trout with a considerable fraction of fine-spotted trout we have encountered is that in Lake Svartavasstjønn. Individuals similar to the intermediate morph in Lake Svartavasstjønn can, however, be found further down the watercourse, but they are very rare. This may be a result of fine-spotted or intermediate individuals descending from Lake Svartavasstjønn, or it may indicate that the fine-spotted morph was more widely distributed earlier.

No statistically significant differences in growth rate between the different morphs were found at any age, nor were there any differences in length–weight ratio (Table 1). The sex ratio shows a predominance of males, varying from 1.30 in the intermediate morph to 3.17 in the fine-spotted morph. The skewed sex ratio may be due to our small sample size. Alternatively, it may be due to differences in behaviour between

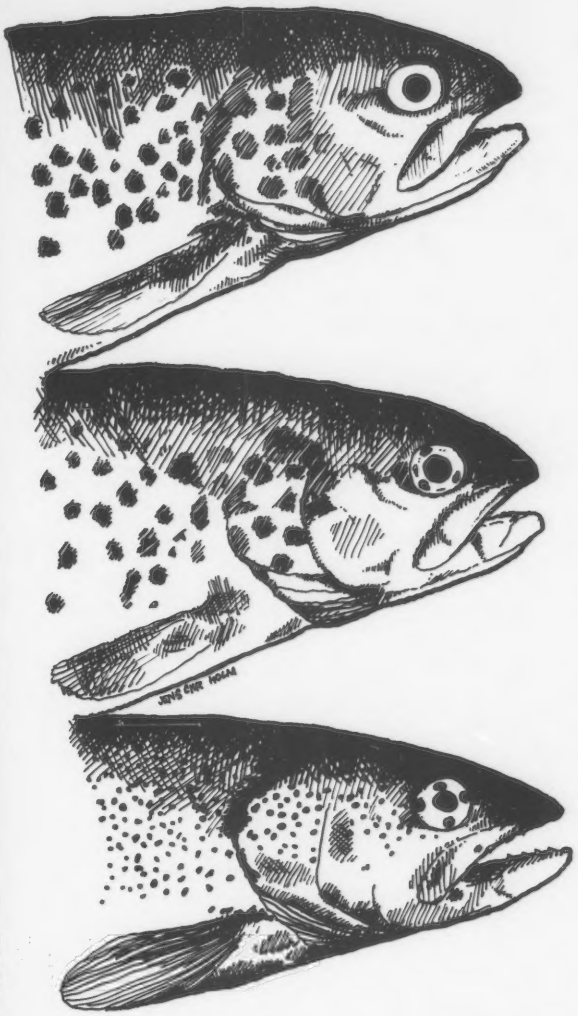

FIG. 2. Spotting characteristics of the three different brown trout morphs in Lake Svartavasstjønn. Top: common large-spotted trout; middle: intermediate morph; bottom: fine-spotted trout (note the four symmetrically located black spots in the eye).

the sexes, for instance the males being more active at the time of sampling (Alm 1959). It is generally known that in anadromous populations of salmonids, migratory behaviour differs between sexes.

Biochemical genetic variation — Only 2 (9.9%) of the 22 loci were polymorphic in the population of brown trout in Lake Svartavasstjønn. Mean heterozygosity calculated over all 22 loci was 2.51%. In *LDH-5* the 105 variant allele was found in high frequency, while the 152 variant allele in *MDH-2* was found in moderately high frequency. In Lake Dragøyfjorden, a variant allele, denoted 50, was also found in *GPD-2*.

The allele frequencies for three loci from the populations in Lake Svartavasstjønn and Lake Dragøyfjorden and a reference population of freshwater resident brown trout from Lake Myrdal

TABLE 1. Number of fish, sex ratio (♂/♀), mean length ±SD, and mean condition coefficient (C.C.) ± SD for the large-spotted, fine-spotted, and intermediate morphs in Lake Svartavasstjønn.

Morph	*N*	Sex ratio	Length (cm)	C.C.
Large-spotted	28	2.11	28.4±6.0	1.04±0.08
Intermediate	23	1.30	27.8±5.8	1.04±0.07
Fine-spotted	26	3.17	27.4±6.0	1.05±0.09

on the Norwegian west coast are compared in Table 2. Both samples from the Hardangervidda area differ significantly (contingency chi-square test) from the Lake Myrdalsvatn sample for all three loci. Most surprising, however, was the very high frequency (0.913) in Lake Svartavasstjønn of the *LDH-5(105)* allele, which has earlier been reported to be a rare allele in other brown trout populations (Ferguson and Fleming 1983; Skaala 1984).

The sample from Lake Dragøyfjorden consisted of only 18 individuals. In spite of low sample size, we found statistically significant differences in the *LDH-5* locus between this sample and the sample from Lake Svartavasstjønn. This indicates a genetic differentiation between the two trout populations in spite of the short distance (3 km) and the lack of any physical barriers.

The individuals in the sample from Lake Svartavasstjønn were grouped according to the morphological classification mentioned earlier. For all three morphs, as well as for the total material, the distribution of genotypes in *LDH-5* was in accordance with the expected Hardy–Weinberg distribution (Table 3). No significant difference in allele frequencies between the different morphs was found.

For *MDH-2*, a deficiency of heterozygotes which was close to significance was detected in the total sample from Lake Svartavasstjønn. As shown in Table 4, this was due to a deficiency of heterozygotes in the group of large-spotted trout. A statistically significant deficiency of heterozygotes is usually interpreted as a mixture of two or more genetically differentiated populations. Although there is no stocking activity in the area today, stocking has been carried out at least once during the last decade. The most probable explanation for the heterogeneity within the large-spotted group of trout is therefore artificial stocking.

The percentage of polymorphic loci is within the range for four other Norwegian populations, where the values ranged from 4 to 22% (Skaala 1984). Nevertheless, the value is low compared with that given by Taggart et al. (1981), who detected polymorphism in 23% of 62 loci in Irish brown trout. This difference may be due to the remote location of the populations reported in this study, as it may be expected that remote populations contain relatively less genetic variation due to founder effects and bottlenecks. The calculated mean heterozygosity of 2.51% also lies within the range of Norwegian populations (Skaala 1984). Again the value in this study is at the low end of the range from 2.3 to 6.2% given by Taggart et al. (1981) estimated for populations of brown trout in Ireland.

The mean heterozygosity found in the fine-spotted brown trout is also comparable with values lor other *Salmo* species which range from 0 (*S. apache*) to 2.4 (*S. salar*) to 4.3 (*S. clarki*) to 6.0 (*S. gairdneri*), as given by Allendorf and Utter (1979).

Ferguson and Fleming (1983) reported that of 116 Irish brown trout populations which they have screened electropho-

TABLE 2. Comparisons of allelic frequencies for *LDH-5*, *MDH-2*, and *GPD-2* for the two lakes sampled and a reference sample from Lake Myrdalsvatn (Skaala 1984) (see also Fig. 1).

Locality	*LDH-5*			*MDH-2*			*GPD-2*			% fine-spotted
	N	*100*	*105*	*N*	*100*	*152*	*N*	*50*	*100*	
Lake Svartavasstjønn	75	0.087	0.913	72	0.736	0.264	75	0.000	1.000	34.7
Lake Dragøyfjorden	18	0.444	0.556	15	0.600	0.400	18	0.083	0.917	0
Lake Myrdalsvatn	96	0.990	0.010	88	0.642	0.358	72	0.188	0.813	0

TABLE 3. Genotype distributions, frequency of *LDH-5(105)* in different morphs, and test for deviation from Hardy-Weinberg equilibrium (BIOSYS-1) (sample from Lake Svartavasstjønn). Contingency chi-square analyses: chi-square = 2.35, df = 2, P = 0.308.

Morph	*N*		Genotypes			Frequency of *105* allelle	Test for Hardy–Weinberg equilibrium		
			100/100	*100/105*	*105/105*		Chi-square	df	*P*
Large-spotted	26	Obs.	0	2	24	0.962			
		Exp.	0.02	1.9	24.0		0.020	1	0.886
Intermediate	23	Obs.	0	5	18	0.891			
		Exp.	0.22	4.56	18.2		0.268	1	0.604
Fine-spotted	26	Obs.	1	4	21	0.885			
		Exp.	0.29	5.41	20.3		2.087	1	0.149
Total	75	Obs.	1	11	63	0.913			
		Exp.	0.52	11.95	62.5		0.513	1	0.474

TABLE 4. Genotype distributions, frequency of *MDH-2(152)* in different morphs, and tests for deviation from Hardy-Weinberg equilibrium (BIOSYS-1) (sample from Lake Svartavasstjønn). Contingency chi-square analysis: chi-square = 2.298, df = 2, P = 0.317.

Morph	*N*		Genotypes			Frequency of *152* allele	Test for Hardy–Weinberg equilibrium		
			100/100	*100/152*	*152/152*		Chi-square	df	*P*
Large-spotted	25	Obs.	4	5	16	0.740			
		Exp.	1.6	9.8	13.6		6.433	1	0.011
Intermediate	23	Obs.	1	7	15	0.804			
		Exp.	0.8	7.4	14.8		0.074	1	0.785
Fine-spotted	24	Obs.	3	10	11	0.667			
		Exp.	2.55	10.89	10.55		0.170	1	0.680
Total	72	Obs.	8	22	42	0.736			
		Exp.	4.9	28.07	38.92		3.530	1	0.06

retically, the *105* allele has been found in frequencies exceeding 0.20 in only 8 populations, all of which were cut off from contact with anadromous brown trout. The authors further reported that the *105* allele has the same electrophoretic mobility as the common *LDH-5* allozyme in Atlantic salmon, rainbow trout, Arctic char, and the Pacific salmons. This indicates that the *105* allele is an ancient allele, and the *100* allele is the result of a mutation occurring in the brown trout lineage. According to Ferguson and Fleming (1983), migratory brown trout fixed for the *105* allele may have colonized rivers and lakes in Britain and Ireland in immediate post glacial times, while a second colonization took place by migratory brown trout characterized by the *100* allele in more recent times.

The frequency of the *105* allele is considerably lower in Lake Dragøyfjorden, 3 km downstream, than in Lake Svartavasstjønn. This observation could be explained by artificial stocking of lower areas by brown trout characterized by the *100* allele, or by a combination of artificial stocking and natural colonization. It may also support Ferguson and Fleming's (1983) hypothesis. We therefore suggest that the Lake Svar-

FIG. 3. Male fine-spotted trout (upper) and female large-spotted trout (lower) captured in Lake Svartavasstjønn, September 1985.

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tavasstjønn area was colonized very early after the retreat of the ice, probably by both fine-spotted and large-spotted trout.

A similar morphological phenomenon, with a fine-spotted population of cutthroat trout, has been described by Behnke (1972), Trojnar and Behnke (1974), and Loudenslager and Kitchin (1979). The taxonomic status of the fine-spotted cutthroat trout is a matter of discussion. According to J. R. Behnke (Colorado State University, Fort Colins, CO 80523, pers. comm.), the fine-potted cutthroat trout is an undescribed subspecies; Loudenslager and Kitchin (1979) did not recognize it as a subspecies because they detected no electrophoretical differences between the fine-spotted and the large-spotted forms.

In the case of the brown trout morphs described here, the data from electrophoresis give no evidence of a significant genetic differentiation between the fine-spotted and the large-spotted forms. This does not mean, however, that we can reject the possibility of a genetic differentiation between the two forms, as we have only studied a limited number of genes, and differentiation may have taken place in other parts of the genome. Further studies have been initiated to distinguish between the two hypotheses. These include breeding studies and collection of ecological and meristic data. According to the information available, the abundance of fine-spotted trout has decreased during the last five decades. This observation illustrates the general need to identify, characterize, and preserve wild populations of salmonids and their potential genetic resources.

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Evidence that Parasitic and Nonparasitic Life History Types are Produced by One Population of Lamprey

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A population of lamprey in a small stream on Vancouver Island, British Columbia, Canada, was shown to contain the nonparasitic *Lampetra richardsoni* and a parasitic variety.

L'auteur montre que la population de lamproies d'un petit cours d'eau de l'île de Vancouver (Colombie-Britannique) se compose de l'espèce non parasite *Lampetra richardsoni* et d'une variété parasite.

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Recently, it was reported (Beamish 1985; Beamish and Withler 1986) that a lamprey in Morrison Creek on Vancouver Island, British Columbia (Fig. 1), was a parasitic variety of the nonparasitic *Lampetra richardsoni*. The variety was parasitic in the laboratory, was unable to survive in seawater, and it lived 1 yr longer than the nonparasitic variety. During that year the parasitic variety increased in size by an average 6.3 cm and 8.0 g (Fig. 2). Allelic frequencies of the parasitic variety were identical to the variety that was believed to be the nonparasitic *L. richardsoni*. The allelic frequencies between the Morrison Creek varieties differed slightly from *Lampetra ayresi* and *L. richardsoni* from other rivers, but the differences were within the range of frequencies observed among the populations sampled. The identical allelic frequencies of the two varieties in the creek suggested that the parasitic variety was not a distinct species. Thus, two distinct life history types appeared to be produced by one population (Fig. 2). I named the parasitic variety *Lampetra richardsoni* var. *marifuga* Beamish, 1985, to facilitate discussion of the two life history types.

Although the presence of the *L. r.* var. *marifuga* was clearly shown, the presence of a nonparasitic variety was not proven. The lamprey identified as *L. richardsoni* could have been spawning individuals of *L. r.* var *marifuga* which in spawning condition could not be separated from spawning *L. richardsoni*. Proof that nonparasitic varieties existed required collecting lampreys in an early stage of metamorphosis and maintaining them in the laboratory until they spawned. Typical *L. richardsoni* would be lamprey that metamorphosed in the summer of one year and matured in the spring of the following year. The parasitic variety would not spawn at this time and would be silver in appearance with prominent dentition.

This note describes the maturation of metamorphosing lampreys collected in Morrison Creek in August 1985. Despite the small size of the sample, the results are reported now, because they confirm that a nonparasitic variety exists in Morrison Creek.

Materials and Methods

Lampreys at an early stage of metamorphosis were collected in Morrison Creek in early August 1985 using electroshockers. They were maintained in a sand substrate in an 800-L tank with flowing fresh water without feeding. Visual examinations were conducted occasionally over a 10-mo period. In early June 1986 they were measured, photographed, examined for sex and maturity, and preserved in Bouin's fixative for 24 h and then transferred to 70% ethyl alcohol. Histological sections were made to confirm the stage of maturity of the parasitic variety.

Results and Discussion

Only four metamorphosing lampreys were collected despite an intensive effort. All four lampreys were at an early stage of metamorphosis. Eyes were developed, but there was no iris. The mouth was oval and contained fimbria. Using the criteria of Potter et al. (1982), these lampreys were about stage 2–3. The lampreys were not examined frequently, to reduce the chance of mortality. At the time of next examination on October 6, 1985, their metamorphosis was completed. They were examined again in early November 1985, March 1986, April 1986, May 1986, and June 1986. Early signs of maturation were first observed in April; by early May, three were mature. One of the lampreys was becoming silver in early March. By early June 1986, three lamprey were in spawning condition and one had the silver coloration of the parasitic variety. The three mature individuals (Fig. 2) were a uniform dark olive brown, had enlarged, closely spaced first and second dorsal fins, and had obsolete dentition. One of the mature lampreys had eggs that were visible through the body wall, another was a mature male, and the third was a maturing female. Since they were obviously mature and ready to spawn, they were preserved as was the silver colored individual.

Histological examination of the silver specimen confirmed the external observations. This male had maturing sperm but no external signs of maturation. The intestine was fully functional, as described in Beamish and Withler (1985) and Beamish and Youson (unpubl. data). Teeth were prominent and well developed. This "silver"form was identical in appearance to the silver-colored lamprey that were parasitic in the laboratory (Beamish 1985; Beamish and Withler 1986). Although this fish was not allowed to feed, there was no doubt that it was the parasitic variety.

The existence of the nonparasitic life history type was demonstrated by the three lampreys that started metamorphosis in late July or early August 1985 and matured and would have spawned in 1986. In the sample of 18 metamorphosed lampreys collected in February 1981 (Beamish 1985), 2 became silver. One of them was preserved and one allowed to feed and the other 16 matured and spawned. While the observations of maturation from both these samples were similar, the February 1981 sample of mature lampreys had completed metamorphosis and theoretically could be the silver or parasitic variety in its second year as an adult. The present study confirms that two distinct varieties occur.

The presence of two life history types, even though *L. r.* var. *marifuga* may feed very little in the stream (Beamish and Withler 1986), and the identical allozyme allelic frequencies strongly suggest the existence of gene flow between the two varieties. Gene flow between the two varieties indicates that one population is producing both nonparasitic and parasitic lamprey. The existence of morphologically distinct varieties with different life history types produced by one population has not been reported for other lamprey populations. It is possible that natural hybridization between *L. ayresi* and *L. richardsoni* had occurred (Beamish and Withler 1986). However, *L. ayresi* is not found anywhere in the Morrison Creek watershed. If natural hybridization occurred, it must have occurred some time ago because the parasitic variety has been observed in the stream each year since 1977. The present population, therefore, must have as part of its genotype the ability to produce both life history types.

The population is considered to be *L. richardsoni* because the nonparasitic variety has a typical *L. richardsoni* life history and normal gonad development, while the parasitic variety has an abnormal sex ratio and abnormal gonad development (Beamish 1985; Beamish and Withler 1986).

The theory that nonparasitic lamprey evolved from parasitic lamprey (Zanandrea 1959; Hardisty and Potter 1971; Vladykov and Kott 1979) is based on the morphological similarity of these paired or satellite species and an overlapping distribution. Recently, I proposed (Beamish 1985) that some nonparasitic species evolved from an intermediate freshwater, parasitic stage, rather than directly from anadromous species. If the theory of an intermediate stage is correct, then it is to be expected that there will be populations of lamprey that produce both parasitic and nonparasitic life history types. The popula-

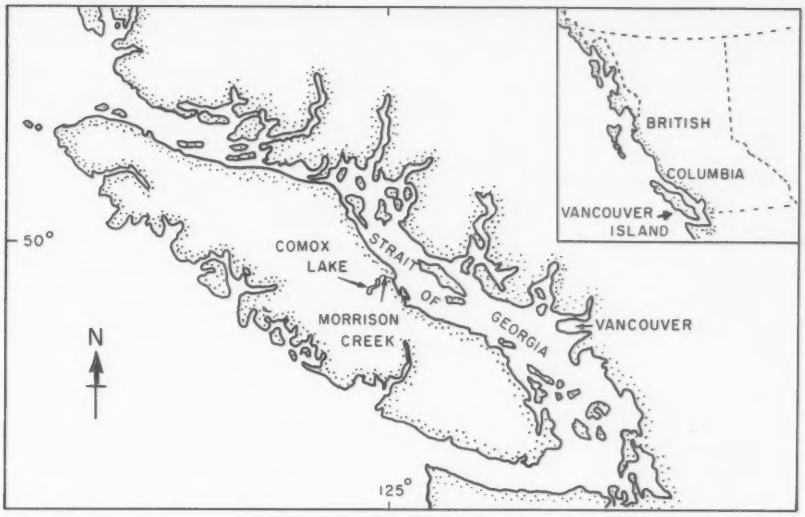

FIG. 1. Location of Morrison Creek.

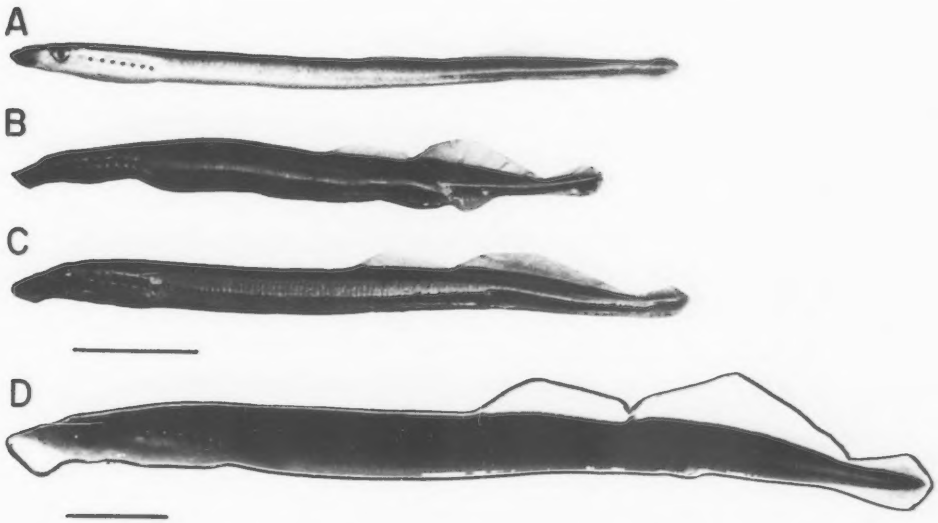

FIG. 2. (A) Male, parasitic variety, showing silver colour and no external signs of maturation. (B) Mature female and (C) mature male *L. richardsoni* from Morrison Creek. Bar = 2 cm. A, B, and C were photographed June 1986 after being held in the laboratory since August 1985. (D) Mature male, parasitic variety, brought into the laboratory in June 1981 and reared to maturity in 1982. Bar = 2 cm.

tion of lamprey in Morrison Creek is the first example of such a population.

There is another study that may be a second example of a population that produces parasitic and nonparasitic life history types. Kux (1965) described *Lampetra* (*Eudontomyzon*) *gracilis* as a new species of nonparasitic lamprey that was paired with the parasitic *Eudontomyzon danfordi*. Kux (1967) maintained ammocoetes in aquaria until they metamorphosed, and in some cases fed, to confirm that two life history types existed. He found that 55% (n = 16) matured without feeding and 45% (n = 13) fed. The lamprey that fed lived 1 yr longer than those that did not. Kux (1967), therefore, used the diameter of the gut and the development of the gonad to separate the parasitic and nonparasitic species.

Recently, Renaud and Holčík (1987) found that *E. gracilis* is indistinguishable from *E. danfordi* and is a junior synonym of *E. danfordi*. They speculated that the proven, nonparasitic behavior of a parasitic species in Kux's experiments was the result of poor feeding conditions. Another explanation is that the population of lampreys sampled by Kux (1965, 1967) was capable of producing both life history types.

In addition, it appears that aspects of the biology of the parasitic *E. danfordi* are similar to the biology of typical nonparasitic species. It is known that the parasitic *E. danfordi*

have large ammocoetes, up to 245 mm (Vladykov 1931). Large ammocoetes are characteristic of nonparasitic species (Vladykov and Kott 1978, 1979). There is no doubt that *E. danfordi* feeds; however, there does not appear to be much growth, suggesting that the amount of feeding is quite limited. Kux (1965) indicated that the size of wild prespawning adult *E. danfordi* ranged from 160 to 245 mm and from 184 to 205 mm in the laboratory (Kux 1967). Renaud and Holčík (1987) recorded the lengths of 90 adults as ranging from 136 to 241 mm. They recorded the lengths of the oldest age groups of ammocoetes as ranging from 166 to 216 mm. Thus, the size of ammocoetes and adults is quite similar. This limited amount growth was confirmed in one of Kux's (1967) experiments in which one *E. danfordi* increased in length from 198 to 203 mm and in weight from 7.8 to 9.2 g during the period of feeding from June until September. The large size of the ammocoetes and the limited amount of feeding on both live and dead fishes (Grossu et al. 1962; Kux 1965, 1967) may be an indication that the *E. danfordi* population is closer to a nonparasitic life history type than a parasitic life history type.

The inability to differentiate adults of either life history type, morphometrically or meristically, the similarity in size, the common occurrence of both life history types in the laboratory experiments, and the apparent similarity in spawning times all indicated that interbreeding could occur. If it occurs, then this is a second example that parasitic and nonparasitic life history types are produced by one population of lamprey.

It is interesting that one female lamprey that spawned but did not feed in Kux's (1967) study was reexamined by Renaud and Holčik (1987) and found to have no secondary sex characteristics. The absence of secondary sex characteristics was observed in silver-colored male *L. r.* var. *marifuga* that, despite the presence of maturing sperm, fed in the laboratory and did not spawn for almost a year (Beamish and Withler 1986).

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Estimation of Fish Length from Acoustic Target Strengths

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Buerkle, U. 1987. Estimation of fish length from acoustic target strengths. Can. J. Fish. Aquat. Sci. 44: 1782–1785.

I show that fish length distributions calculated from acoustic target strengths of cod (*Gadus morhua*) are in error when target strength–length relationships are used that do not account for the orientation distribution of the fish. The magnitude and statistical significance of the errors vary with the length frequency structure of the fish sample and are thought to be large enough to question the value of acoustically determined lengths in fish surveys if corrections for fish orientation are not applied.

On montre que les distributions des longueurs des poissons calculées à partir des indices de réflexion des cibles acoustiques de morue (*Gadus morhua*) sont erronées lorsqu'on utilise des relations entre l'indice de réflexion et la longueur qui ne tiennent pas compte de la répartition de l'orientation des poissons. La grandeur et la signification statistique des erreurs varient selon la structure des fréquences de longueur des

poissons échantillonnés et semblent suffisamment importantes pour mettre en doute les valeurs des longueurs déterminées par relevés acoustiques des poissons si l'on n'applique pas de correction afin de tenir compte de l'orientation des poissons.

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The development of dual-beam and split-beam echo sounding equipment has made it possible to determine directly the in situ target strength of fish that can be resolved as single targets (Traynor and Ehrenberg 1979; Foote et al. 1985). This is a great advance for acoustic estimation of fish abundance because the in situ target strengths can be combined with estimates of mean weight per fish in catch samples to obtain the estimate of target strength per kilogram that is needed to convert measurements of acoustic scattering to estimates of biomass. The ability to determine in situ target strengths and the well-known dependence of target strength on fish length (Middtun and Hoff 1962; Love 1971; Goddard and Welsby 1977; Nakken and Olsen 1977) have also led to the idea of determining fish length from acoustic data (Ehrenberg 1974; Dickie et al. 1983, 1984).

Target strength, however, is not a function of fish length alone. It also depends on the species and the aspect in the sound beam, the depth and depth acclimation, as well as condition factors that may include reproductive state, stomach and fat content, and anything else that affects the reflective properties of fish. Among these factors, aspect has received the most attention. Middtun and Hoff (1962) and Nakken and Olsen (1977) presented dorsal aspect target strength functions for individual fish showing that target strength can vary by a factor of 100 with changes in tilt angle of 10°. An equation relating average target strength of numbers of cod to length and aspect (Buerkle and Sreedharan 1981) showed that average target strength can change with aspect by a factor of 30 with tilt between ±45° (+ denotes head above, − denotes head below horizontal plane).

It is now recognized that using target strength – length relationships that are not averaged for the appropriate tilt angle distribution of the fish can result in large errors in estimates of acoustic abundance (Foote 1980). Similarly, using target strength – length relationships that are not averaged for the appropriate tilt angle distribution of the fish will result in large errors in estimates of fish length from acoustic data.

This note examines the effect of using the target strength – length relationship of cod (*Gadus morhua*) in horizontal aspect to estimate the length of fish with tilt angle distributed as observed in free-swimming fish.

Materials and Methods

The tilt angle distribution of free-swimming cod photographed by Olsen (1971) was estimated to have a mean of −4.4° and a standard deviation of 16° (Foote 1980). The target strength distributions resulting from this tilt angle distribution were calculated for cod in three discrete length classes and for two hypothetical length distributions using experimental data of target strength – length – aspect (Buerkle and Sreedharan 1981). The target strength distributions were then converted to length distributions using the target strength – length relationship of the cod at horizontal aspect.

The equation relating target strength of cod to fish length and aspect (Buerkle and Sreedharan 1981) included a small error and is recalculated for this work as

$$(1)\quad TS = 27.4 \log L - 4.3 \sin(2P) + 7.2 \cos((2P) + 5.9(\cos P \cos R)^2 - 95.3$$

where TS is target strength (decibels), L is fish length (centimetres), and P and R are tilt and roll angle of the fish, respectively. This equation accounts for 74.1% of the variation in the measurements, with 29.6% accounted for by length and 44.5% accounted for by aspect. Since the remaining 25.9% of the variation includes inherent differences in target strengths of individual fish due to physiological differences, as well as the measurement errors in aspect length and target strength, there is probably little error due to the fitted model.

For fish at uniformly horizontal aspect, tilt and roll are 0° and equation 1 reduces to

$$(2)\quad TS = 27.4 \log L - 82.2$$

and since the model is thought to introduce little error, length is related to target strength by

$$(3)\quad L = 10^{\frac{(TS + 82.2)}{27.4}}.$$

The tilt angle distribution of free-swimming cod is taken as in Foote (1978) to be a truncated Gaussian distribution by the probability density function

$$(4)\quad f(\theta) = \begin{cases} \dfrac{1}{\sigma_\theta \sqrt{2\pi}} \exp - \dfrac{(0 - \bar{\theta})^2}{2\sigma_\theta^2} & \text{for } -3.32 < \theta - \bar{\theta} < 3.20 \\ 0 & \text{for } -3.32 > \theta - \theta > 3.20 \end{cases}$$

where θ is tilt angle P, $\bar{\theta}$ is mean tilt angle −4.4°, σ_θ is the standard deviation 16°, and the truncation is this case is at −57.5° and 47.5°.

Probabilities of tilt were estimated in 21 classes of tilt (class interval 5°) as $5 \times f(\theta)$, with θ equal to the class midpoints.

Target strengths at the 21 tilt class midpoints were calculated for each actual fish length class by equation 1. For presentation of target strengths the probabilities were summed in 2-dB class intervals of target strength. Apparent lengths were calculated from target strength by equation 3.

The probabilities in apparent length classes are the products of the probabilities of the input length class (1.0, in the three discrete length classes) and the probabilities from the tilt angle distribution summed in 3-cm class intervals of fish length.

Results and Discussion

The target strengths of cod 23.5, 35.5, and 47.5 cm long oriented horizontally are −44.6, −39.7, and −36.3 dB, respectively (equation 2). If these cod were oriented like free-swimming cod (Olsen 1971) with mean tilt of −4.4° and standard deviation of 16°, their target strengths would be distributed as in the three distributions of Fig. 1.

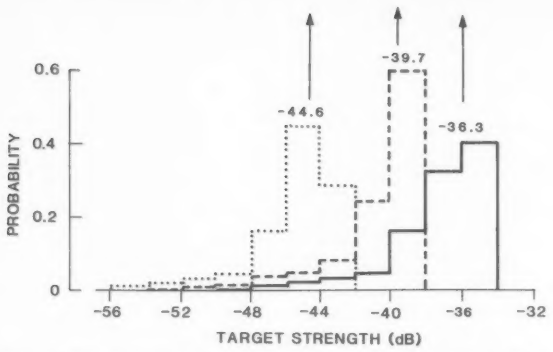

FIG. 1. Target strengths of three lengths of cod (as in Fig. 2) at horizontal aspect (numbers at arrows) and the target strength distributions of the same fish oriented with mean tilt −4.4° and standard deviation 16°.

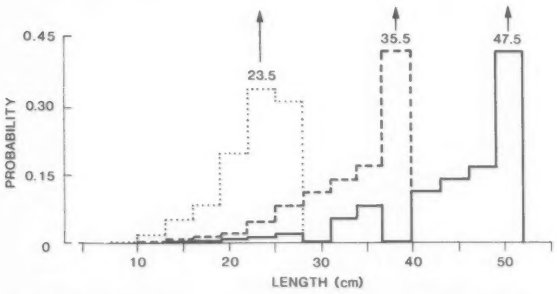

FIG. 2. Length distributions calculated from target strength distributions of three lengths (numbers at arrows) of cod oriented with mean tilt −4.4° and standard deviation 16°.

With one exception, the effect of the tilt angle distribution is to spread targets to lower target strength classes. This effect can be explained by the asymmetries of the target strength function and the tilt angle distribution. If both maximum target strength and mean tilt angle were at 0°, the effect of tilt angle distribution would be only a decrease in target strengths. With a mean tilt angle of −4.4° and the maximum target strength occurring at −13° (equation 1), however, some fish in the distribution will have target strengths that are higher than those at 0° tilt. Acoustic scattering from individual live fish has also been shown to fit a range of Rician probability density functions (Clay and Heist 1984). The functions vary from Rayleigh distributions for wildly swimming fish to normal distributions for very calm fish. Including such functions in these calculations would increase the spread of the target strength distributions but would not alter the general character.

Fish lengths calculated from the target strengths by equation 3 appear as in Fig. 2. These apparent length distributions have modal classes that include the actual lengths, but the actual length makes up only about 30–40% of the apparent lengths. With one exception the remaining apparent length classes are shorter than the modal class. The mean lengths of the apparent length distributions are 22.4, 33.8, and 45.1 cm for the actual lengths of 23.5, 35.5, and 47.5 cm, respectively. Apparent mean lengths are 5% shorter than actual lengths.

The probabilities shown as 0 in two of the apparent length classes show a discreteness problem with approximating probabilities at 5° increments in the tilt angle distribution, and can be ignored.

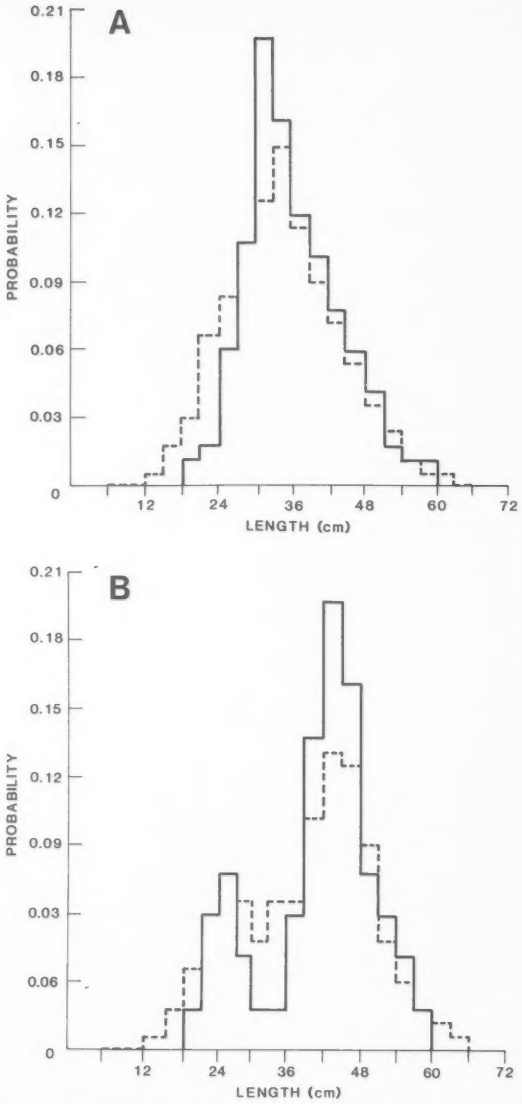

FIG. 3. (A) Unimodal and (B) bimodal length distributions (solid line) and apparent length distribution (broken line) of the same fish calculated from the target strength distribution.

These simple examples point out that a distribution of tilt angles, as occurs in nature, results in distributions of target strength that are biased low in terms of horizontal aspects target strengths, and are not good estimators of fish length in terms of horizontal aspects target strength – length relationships.

Naturally occurring fish length distributions are more complex in structure, and the effect of tilt angle distribution on apparent lengths estimated from target strengths will be obscured to various degrees. It is informative, therefore, to examine the effect in some realistic fish length distributions that could occur on the Scotian Shelf. An actual unimodal length

TABLE 1. Frequencies (f) of apparent lengths calculated from target strengths of a unimodel and a bimodal fish length, distribution with actual frequencies (F) and a sample size of 200.

Length class (cm)	Unimodal		Bimodal	
	F	f	F	f
6–8.9		0.05		0.10
9–11.9		0.42		0.56
12–14.9		1.73		1.61
15–17.9		3.35		3.47
18–20.9	2	6.28	4	7.29
21–23.9	4	13.25	12	12.46
24–26.9	12	17.10	16	12.26
27–29.9	22	21.67	8	12.65
30–32.9	40	25.26	4	9.74
33–35.9	32	30.22	4	13.01
36–38.9	24	22.85	12	13.63
39–41.9	20	17.41	28	19.84
42–44.9	16	14.29	40	26.67
45–47.9	12	10.20	32	25.57
48–50.9	8	7.24	16	18.48
51–53.9	4	4.34	12	9.93
54–56.9	2	1.91	8	5.79
57–59.9	2	1.15	4	3.52
60–62.9		0.84		2.55
63–65.9		0.43		0.87

distribution and the apparent length distribution calculated from its target strength distribution differ (Fig. 3A). The apparent length distribution has a lower peak and, generally, a decrease in probabilities on the right side of the peak and an increase in probabilities in the left side of the peak. In the case of actual and apparent bimodal length distributions (Fig. 3B), the pattern in the shift in probabilities is obscured even more but is obvious nonetheless.

In actual situations of estimating fish lengths from target strengths, the calculations are based on many hundreds of measurements (Dickie et al. 1983, 1984). For comparison with a real situation, and to enable an estimate of the significance of the difference between the apparent and the given length distributions, it is reasonable and even conservative to convert the probabilities in Fig. 3A and 3B to frequencies of sample size 200. The results are shown in Table 1.

The chi-square calculated for the 14 length classes where the given frequencies (F) are not 0 is 39.6 for the unimodal distribution and 44.6 for the bimodal distribution. The differences between the apparent length distributions and the given length distributions are statistically very highly significant ($p < 0.001$).

It is reasonable to expect a spread in tilt angles to effect a significant shift in small length classes. It has been suggested (S. Gavaris, Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B., pers. comm.) that acoustic estimation of numbers of fish in only two length range groups would be useful. The length groups suggested for cod were fish shorter than 30 cm and fish longer than 30 cm.

To investigate this potential, both unimodal and bimodal given distributions were selected to have 40 fish shorter than 30 cm and 160 fish longer than 30 cm (Table 1). The corresponding numbers in the apparent length distributions are 64 and 136 for the unimodal distribution and 50 and 150 for the bimodal distribution. That is an increase of 60% of the shorter fish in the unimodal distribution and an increase of 25% of the shorter fish in the bimodal distribution. For the larger fish, the change is a decrease of 15% in the unimodal distribution and a decrease of 6% in the bimodal distribution. The chi-square for the change in frequencies is 18.0 for the unimodal distribution with $p < 0.001$. The chi-square for the bimodal distribution is 3.12 with $p < 0.10$.

These distributions show that the amount of change and the statistical significance vary with the shape of the distribution, and that target strength, without tilt angle correction, is not a good criterion for grouping fish by length, even into wide length classes. The effects demonstrated also have more general significance. In surveys, in particular where each species has its own target strength – length – aspect function and where species mix and orientation distributions are likely to change with time and locality, fish length distributions estimated from target strengths must be considered to be of questionable value. Adequate estimates of species and length compositions can be obtained only by biological sampling.

The weighted means of the apparent lengths were 34.5 cm for the unimodal distribution and 38.9 cm for the bimodal distribution. That is 1.6 and 1.9 cm shorter than the weighted means of the respective actual distributions. The differences, however, are not significant and estimation of mean lengths from target strengths uncorrected for fish tilt angle may be useful in some situations.

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Precision Micrometer Measurement of Mouth Gape of Larval Fish[1]

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Arts, M. T., and D. 0. Evans. 1987. Precision micrometer measurement of mouth gape of larval fish. Can. J. Fish. Aquat. Sci. 44: 1786–1791.

A precision micrometer device is described which standardizes measurement of mouth gape of larval fish and provides a greater degree of accuracy and speed than the conventional manual method. We compared gape measurements of larval lake whitefish (*Coregonus clupeaformis*) and lake herring (*Coregonus artedii*) using the gape micrometer versus the manual method. The micrometer measurements revealed a greater increase in gape with body length and resulted in a greater proportion of the variance in gape being explained, indicating that the gape micrometer is more sensitive and accurate than the manual method. Coefficient of variation of gape measurements on 238 larval yellow perch (*Perca flavescens*) decreased with body size from 0.5–4.0% at 0.8–1.2 cm standard length to 0.2–0.5% at 3.0 cm. The device has the added advantage that it could be adapted to connect to a microcomputer for direct data capture.

On décrit un micromètre de précision qui normalise la mesure de l'ouverture de la bouche de poissons larvaires et fournit un degré plus élevé de précision et d'efficacité que la méthode manuelle classique. On a comparé les mesures de l'ouverture de la bouche de larves de grand corégone (*Coregonus clupeaformis*) et de cisco de lac (*Coregonus artedii*) obtenues à l'aide du micromètre et de la méthode manuelle. Les mesures au micromètre ont révélé une plus grande augmentation de l'ouverture de la bouche en fonction de la longueur du corps et ces résultats ont permi d'expliquer une plus grande partie de la variance de l'ouverture de la bouche, ce qui indique que le micrométre est plus sensible et plus précis que la méthode manuelle. Le coefficient de variation des mesures de l'ouverture de la bouche de 238 larves de perchaude (*Perca flavescens*) diminuait en fonction de la taille du corps pour passer de 0,5–4,0 %, à 0,8–1,2 cm de longueur standard, à 0,2–0,5 %, à 3,0 cm. Ce dispositif présente un autre avantage : on peut l'adapter et le relier à un micro-ordinateur pour la collecte directe des données.

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Because mouth gape largely determines maximum prey size of larval and juvenile fish, precise measurement of gape has the potential of giving information on the capacity of fish to handle prey of different size. Traditionally, gape has been determined by manually spreading the jaws with forceps and measuring with either an ocular micrometer (Hartman 1958; Wankowski 1979; Mathias and Li 1982) or vernier caliper (Northcote 1954). These methods are awkward and subject to measurement error due to inability to hold fish steady, subjective interpretation of what is a normal open-mouth position, and differences in technique between individuals. Very small fish (<10 mm total length) simply can not be effectively measured.

Wong and Ward (1972) inserted a calibrated, tapered brass cone into the mouth to measure gape. This device was difficult to hold, allowed measurement increments of only 0.2 mm, could not easily accommodate fishes with different head lengths, and was not designed to be used with a dissecting microscope or microcomputer. Therefore, we developed a device that uses the design principle of Wong and Ward (1972), but circumvents these problems.

At maximum gape, the dorso-ventral dimension of the mouth is usually greater than the lateral dimension, specially in fish such as *Lepomis* spp. which are greater in depth than breadth. Wankowski (1979), for example, found that the dorso-ventral dimension of juvenile Atlantic salmon (*Salmo salar*) was 1.5 times greater than the lateral dimension at maximum gape. The gape micrometer device, with its conical tips, measures the smallest internal dimension, whether vertical or horizontal, at maximum gape. We make the assumption that this dimension represents the maximum ingestable particle size for a fish larva of a given length and thus provides an ecologically meaningful measurement.

Methods

Description of the gape micrometer — The gape micrometer (Fig. 1 and 2) consists of three basic components: Plexiglas body; micrometer scale (Mitutoyo Co. model 150-192) with attached measurement head; and removable stainless-steel rods with conical tips that serve to hold the mouth of the fish in a fixed, open position during measurement. Two measuring rods

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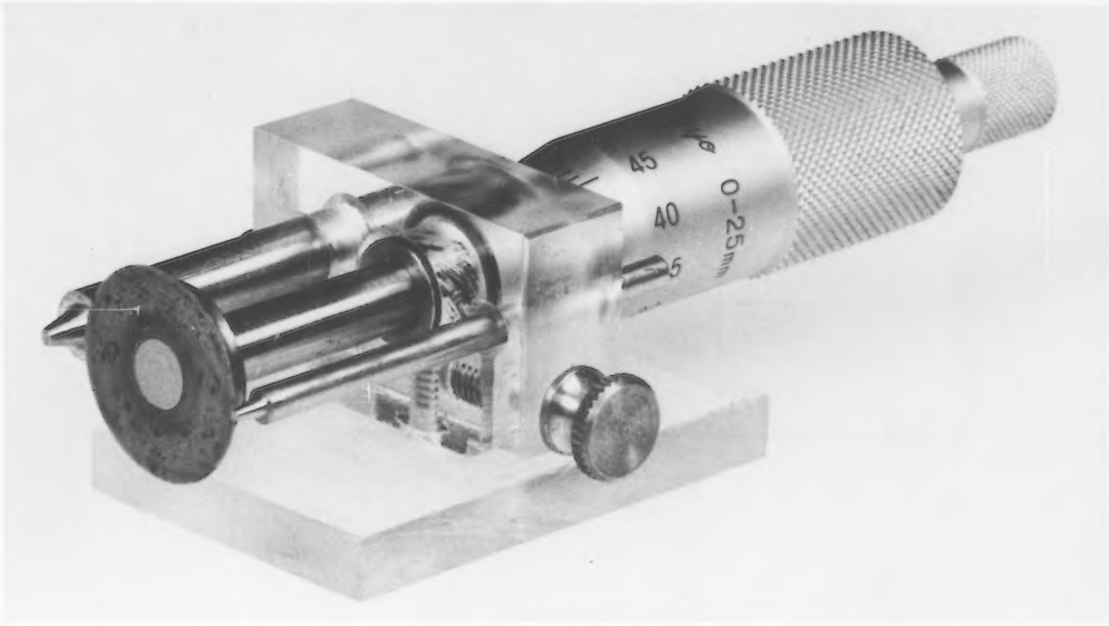

FIG. 1. Gape micrometer showing details of the measuring cones and micrometer head.

at a time are mounted in the gape micrometer and are locked in position by brass set-screws. In total, a set of six interchangeable measuring rods were produced, the conical tips of which were machined to an accuracy of 0.005 mm of their nominal diameters. The tips and basal diameters (millimeters) of the six measuring cones are 0–1.0, 0.5–1.5, 1.0–2.0, 1.5–3.5, 2.5–4.5, and 3.5–5.5 mm, ±0.005 mm, providing a measurement range for gape from 0.005 to 5.5 mm.

Calibration procedure — The principle of the measurement method is that the mouth shape of a small fish is approximated by a circular diameter and that the diameter of a "cone at any point along its height is a simple geometric function of linear distance from the apex to that point. In operation, two measuring rods, having appropriate conical diameters for the specimens to be measured, are inserted into the device. The micrometer is set to zero and the tips of the measuring cones are aligned exactly with the flat surface of the micrometer head. This is best accomplished by placing a flat object, such as a glass microscope slide, against the surface of the micrometer head. The rods can then be moved forward until they butt up snugly against the slide at which point the brass set-screws are tightened. Now, the linear distance of travel by the micrometer head moving alongside the fixed cones can be related to the diameter of the cones at any desired point. Calibration tables were prepared for each cone so that the micrometer reading could be quickly converted to cone diameter which is in turn equivalent to gape.

Measurement of gape — Once calibrated as above, a fish is placed on the device by sliding the mouth over the appropriate measuring cone under a dissecting microscope. The fish is pushed forward on the cone until firm resistance is encountered. Flared operculi or the fish sliding back down the cone were indicative of inserting the cone too far into the mouth.

The micrometer is then adjusted until the flat surface of the micrometer head is directly opposite the corner of the upper and lower jaw. The micrometer reading is then found on the calibration chart and cone diameter (gape) is read and recorded. A choice of two cones for each fish simply provides some flexibility in selecting the cone of appropriate size for a particular specimen.

Performance assessment — The gape micrometer was used to measure 238 larval yellow perch (*Perca flavescens*) varying in standard length from 0.7 to 3.1 cm. Five replicate measurements were made on each fish and coefficients of variation of the measurements were related to fish body length.

Specimens of larval lake whitefish (*Coregonus clupeaformis*) and lake herring (*Coregonus artedii*) were measured by the conventional manual method and then remeasured using the gape micrometer. Analysis of covariance was used to test for differences between regressions of gape versus standard lengths for the two methods derived from the same test fish. The larvae were captured using surface trawls and fixed in 10% formalin prior to measuring.

Results and Discussion

Standard length explained 98% of the variance in mouthgape of the yellow perch larvae (Fig. 3). Coefficient of variation using the gape micrometer varied from 0.2 to 4.5%, but was highest for small larvae (0.5–4.0% at 0.7–1.8 cm standard length) and smallest for the large larvae (0.2–0.5% at 3.0 cm) (Fig. 4). Two or three replicate measurements should be made for larvae less than 2.0 cm and one or two measurements for fish greater than 2.0 cm. Stretching of the mouth occurred with repeated measurement in all three species, but was insignificant when five or fewer replicates were involved (pairwise t-test, $\alpha = 0.05$). Preservation in formaldehyde does increase the

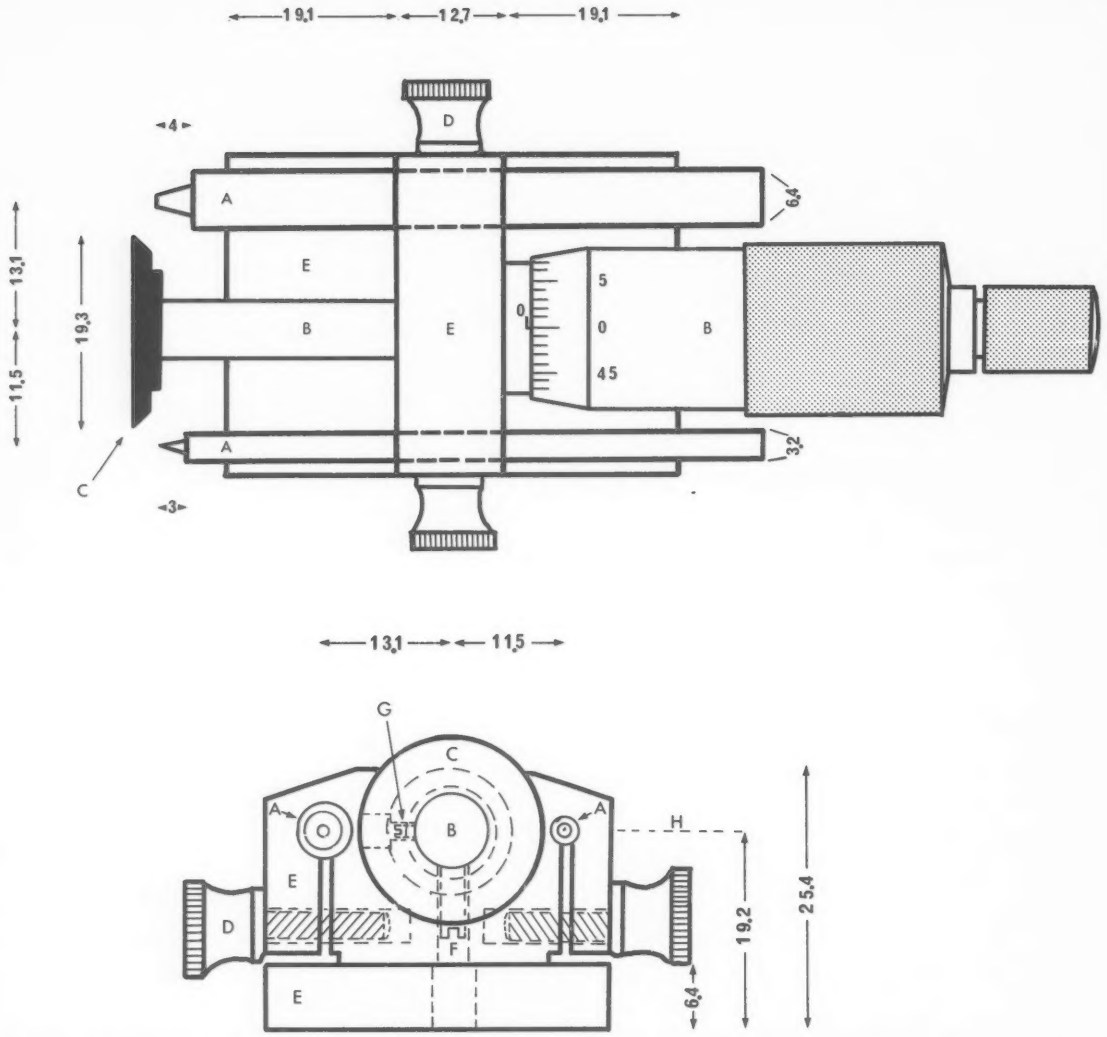

FIG. 2. Top and end views of gape micrometer. All measurements in millimeters. A, Stainless steel rods (only two shown); B, micrometer body; C, micrometer head; D, brass set-screw; E, Plexiglas body; F, micrometer body set-screw; G, micrometer head set-screw; H, plane of focus.

TABLE 1. Summary statistics for regressions of gape (mm) versus standard length (cm). C = conventional gape measurement; GM = gape micrometer. Analyses of covariance were used to test for differences between the slopes.

Species	Lake	Measuring device	n	Slope	Intercept	R_2	Prob.
Whitefish	Simcoe	C	29	0.86	−0.31	0.89	$p < 0.005$
		GM	38	1.18	−0.75	0.96	
Herring	Opeongo	C	48	0.71	−0.14	0.94	$p < 0.001$
		GM	48	1.09	−0.55	0.97	
Perch	Opeongo	GM	238	1.53	−0.52	0.98	

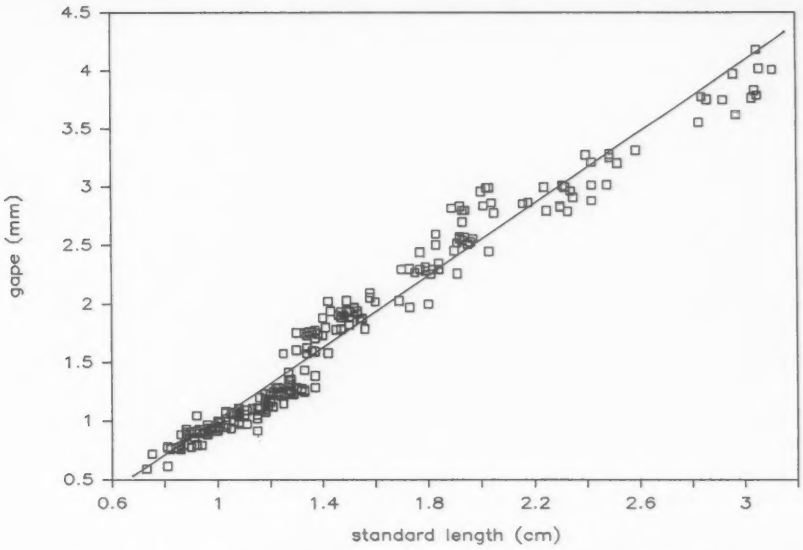

FIG. 3. Mouth gape versus standard length for yellow perch larvae from Opeongo Lake.

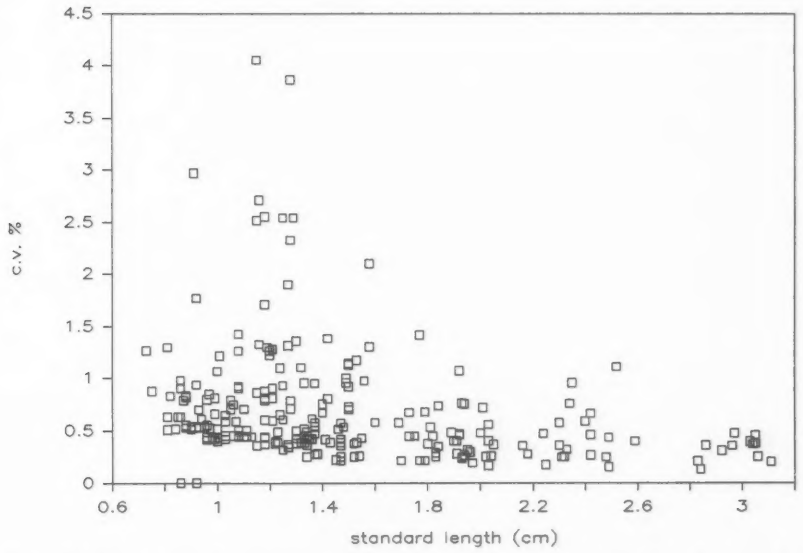

FIG. 4. Relative variation of gape measurement as estimated by the coefficient of variation for a sample of 238 perch larvae differing in body length.

stiffness of the fish, so that ideally, measurements should be made on fresh fish anesthetized with MS222 (ethyl-*m*-aminobenzoate methanesulfonate).

Regression of gape versus standard length for lake whitefish and lake herring larvae revealed greater slopes and smaller residuals for the gape micrometer measurements than for the conventional method (Table 1). Gape measurements using the two methods diverge mainly for fish of larger body sizes (Fig. 5a and 5b). The conventional method, however, appears to overmeasure the gape of small larvae and to undermeasure the gape of larger larvae, suggesting that the gape micrometer provides greater measurement sensitivity.

The gape micrometer improves upon the method of Wong and Ward (1972) because the theoretically unlimited cone configurations allow measurement over a broad range in mouth gapes and fish species. The short height of the cones usually prevents the tip of the cone from reaching the back of the fish's mouth before the fish is fully mounted on the cone. Overlapping measuring ranges of the cones is an additional safeguard, since the same fish can be measured on a larger cone with less taper.

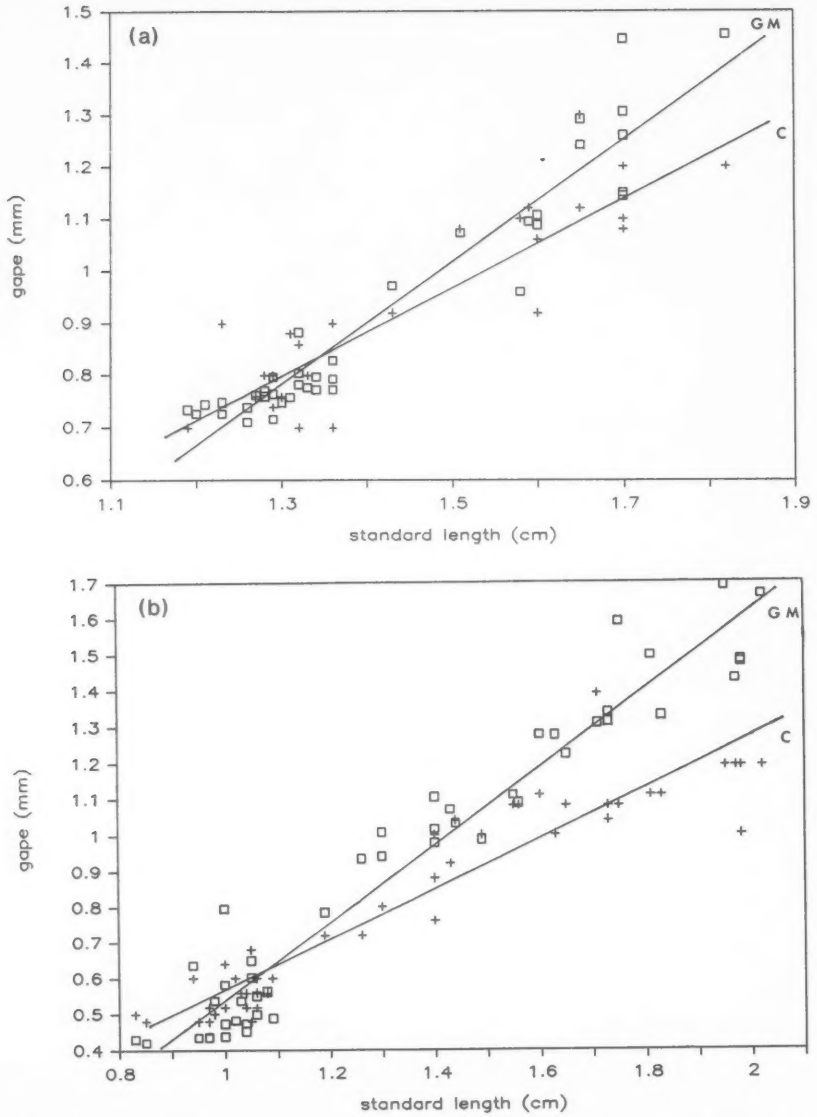

FIG. 5. Comparison of the conventional (C) (see text) and the gape micrometer (GM) methods of measurement for (a) larval whitefish from Lake Simcoe and (b) larval herring from Opeongo Lake. Lines shown are model I regressions. □ GM; +. C.

The gape micrometer improves measurement under a microscope because the measuring rods are part of a rigid Plexiglas body that can be fixed to the stage of the microscope and because the interchangeable cones are always in the same focal plane (see H, Fig. 2) when mounted in the device. The micrometer head also passes very close (<0.55 cm) to the actual measuring cones, increasing accuracy. An additional advantage of the gape micrometer is that it could potentially be adapted to connect to a personal computer in a manner similar to caliper systems (e.g. Sprules et al. 1981). Finally the gape micrometer is small and convenient to use, and is relatively inexpensive. The cost of our prototype model was less than $50.00 (Canadian) for materials.

Mouthgape of larval fishes increases relatively rapidly and changes in shape as the larvae metamorphose. Precise knowledge of these changes during development is of basic interest with reference to the feeding ecology and survival of the larvae under changing biotic and abiotic conditions. Use of the gape micrometer to precisely follow changes in the size of the mouth gapes of larval fish may add significantly to understanding the

factors influencing their survival. Application of this device to problems of artificial feeding as well as determination of maximum diet particle sizes for other species having tiny pelagic larvae may also prove useful.

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A Note on Variability of Marine Survival of Sockeye Salmon (*Oncorhynchus nerka*) and Effects of Flooding on Spawning Success[1]

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Thorne, R. E., and J. J. Ames. 1987. A note on variability of marine survival of sockeye salmon (*Oncorhynchus nerka*) and effects of flooding on spawning success. Can. J. Fish. Aquat. Sci. 44: 1791–1795.

Most of the annual variability in sockeye salmon (*Oncorhynchus nerka*) survival has been assumed to be associated with freshwater stages, while marine survival has been assumed to be very consistent from year to year. Data from Lake Washington sockeye salmon stock, including hydroacoustic surveys of presmolt populations, indicate that marine survival may vary on the order of 4–20%. However, the data also show that river flow conditions during spawning and gravel incubation have a major effect on production for this stock.

On a supposé que la plus grande partie de la variabilité annuelle de la survie du saumon nerka (*Oncorhynchus nerka*) était liée aux stades dulcaquicoles tandis que la survie en milieu marin a été supposée uniforme d'une année à l'autre. Des données sur le stock de saumon nerka du lac Washington, y compris des relevés hydroacoustiques des populations de pré-smolts révèlent que la survie en mer peut varier de 4 à 20 %. Toutefois, les données indiquent aussi que le débit des cours d'eau pendant le frai et l'incubation a une incidence importante sur la production.

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The historical view among those concerned with sockeye salmon (*Oncorhynchus nerka*) management has been that mortality in the freshwater environment is not only much greater, but also much more variable than that in the ocean environment (Foerster 1968). Consequently, predictions of run size and enhancement activities have focused on the freshwater phase of the sockeye life history. Imprecise forecasts have been attributed to lack of adequate data on smolt outmigrations, and indeed there are uncertainties associated with the commonly used techniques: fyke nets, weirs, and inclined plane traps. Consequently, few data are available to examine the hypothesis that marine survival is consistent (Mathews 1984). Further, lack of good data on the magnitude of smolt outmigrations has limited our understanding of the factors that affect production in freshwater. One particular factor that can impact production is flooding during the time that the eggs are in the gravel (McNeil 1966). The purpose of this note is to present a set of data from Lake Washington, near Seattle, that indicates considerable variability in marine survival and shows that flooding can be the major factor affecting smolt production.

Hydroacoustic Surveys on Lake Washington

Lake Washington was a site of initial investigations into the utility of hydroacoustic techniques for population assessment (Thorne 1970). The first presmolt population estimate using echo integration techniques was made in 1969. Subsequently, over 40 hydroacoustic surveys of juvenile sockeye salmon have been made on Lake Washington, including annual estimates of presmolt populations since 1969 (Thorne and Thomas 1984). Detailed descriptions of the methodology of these surveys as well as other fishery data on the Lake Washington run are given in several publications, including Thorne (1972), Thorne et al. (1975), Traynor (1973), Bryant (1976), and Thorne (1983a).

As a result of these investigations, a set of data including estimates of smolt outmigration and subsequent adult run size for sockeye salmon brood years 1967–79 is available from numerous Washington Department of Fisheries (e.g. Anonymous 1978) and Fisheries Research Institute publications (e.g. Dawson and Thorne 1978). Examination of these data indicates that marine survival varies annually from 4.0 to 20.1% (Table 1).

Obviously the use of these data to infer marine survival depends on the precision and accuracy of both the estimates of adult stock size and the hydroacoustic estimates of smolt outmigration. Several aspects of Lake Washington and its sockeye salmon stock greatly simplify the problems of adult stock estimation. The stock has very little exposure to mixed-stock fisheries. Most harvest occurs in the immediate terminal area, including a well-monitored sport fishery within the lake itself. Entrance to Lake Washington is restricted to the Hiram Chittenden locks. All sockeye entering the locks are counted. The accuracy of this count has been thoroughly evaluated by a combination of alternative techniques, including hydroacoustic surveys and tower counts. Thorne (1979) showed only a 2% difference among estimates from hydroacoustics, tower counts, and the total lock count over a 4-yr period. Bryant (1976) detailed the techniques used to obtain the statistics on the stock, both adult and juvenile.

Verification of Hydroacoustic Estimates

Error associated with hydroacoustic estimates of juvenile sockeye can be caused either by random or systematic sources (Thorne 1983b). Error from random sources is associated with sampling a non-uniform fish distribution, and its magnitude can readily be incorporated into confidence intervals. Although many of the early studies did not include confidence interval determinations, several subsequent studies have considered the degree of uncertainty associated with the hydroacoustic estimates on Lake Washington from these sources (Traynor 1973; Thorne 1983a). Confidence intervals (95%) are typically ±35% for a single unreplicated survey, but improve to ±15% for replicated surveys. Most surveys listed in Table 1 were replicated.

The amount of error from systematic sources associated with the techniques is more difficult to ascertain because of the limitations of alternative assessment techniques (Thorne 1987). Three different approaches have been taken to validate the hydroacoustic results: (1) direct synoptic comparisons of hydroacoustic density measurements and net catches, (2) comparisons of annual hydroacoustic estimates of the total lake sockeye salmon population with corresponding estimates derived from trawling, and (3) evaluation of the reasonableness of the annual smolt estimates by other predictors of sockeye production in the freshwater phase. This third approach revealed the importance of flood conditions.

An advantage of Lake Washington compared with most sockeye salmon nursery lakes is that it is accessible to large vessels so that efficient midwater trawl net sampling can be used for species identification in association with the hydroacoustic surveys. The net used on Lake Washington was a 3-m IKMT (Isaacs and Kidd 1953) towed at over 2.5 m/s. Typically, 20–30 tows were made each survey. During the initial development of the hydroacoustic techniques, many direct comparisons were made between net catches and synoptic hydroacoustic measurements of fish density along the trawl path. Figure 1 (from Thorne et al. 1975) is a typical example of these results. Many other similar comparisons have been made between the hydroacoustic techniques and trawl catches. The conclusion is that hydroacoustic techniques provide estimates of fish abundance that compare well on a relative basis with midwater trawl catches when conditions such as ambient light and water clarity are constant, so that net catchability is reasonably constant (Thorne 1983b, 1987).

The net sampling on Lake Washington is done at five sampling locations (Thorne et al. 1975). In addition to the direct synoptic comparison between hydroacoustic observations and net catches, the population estimates from the hydroacoustic surveys in Lake Washington were compared with corresponding weighted mean catches, with weighting by the surface area associated with each of the five sampling areas. Details are given in Traynor (1973). The results again indicate that hydroacoustic results compare favorably with abundance indices provided by the midwater trawling (Fig. 2).

Effects of Flooding

The third approach to validate the hydroacoustic results is to compare the hydroacoustic measurements of smolt outmigration with other techniques for predicting smolt production. The underlying basis for most sockeye salmon management is a spawner–recruit relationship that assumes that the production is a linear function of the number of spawners until the spawning population reaches a level where density-dependent sources of mortality take effect (Ricker 1954). These sources include the amount and quality of gravel for spawning and the carrying

TABLE 1. Presmolt population estimates and associated run characteristics for 1967–78 brood years, summarized from Washington Department of Fisheries and Fisheries Research Institute reports.

Brood year	Presmolt estimate		Parent population ($\times 10^3$)	Resulting adult run size ($\times 10^3$)	Marine survival (%)	Presmolts per spawner
	Date	($\times 10^6$)				
1967	Feb. 1969	7.5[a]	383	559	7.5	19.6
1968	Feb. 1970	3.2	252	299	9.4	12.7
1969	Mar. 1971	3.8	200	476	12.5	19.0
	Apr. 1971	3.6				
1970	Mar. 1972	2.0	124	150	7.5	16.1
1971	Feb. 1973	1.7	183	144	8.5	9.3
1972	Mar. 1974	3.6	249	180	5.0	14.4
1973	Nov. 1974	4.1	330	593	—	—
	Mar. 1975	1.9[b]				
1974	Feb. 1976	0.8[b]	126	311	—	—
1975	Mar. 1977	1.1	148	229	20.1	5.6[c]
1976	Feb. 1978	4.0	159	500	12.6	24.9
1977	Feb. 1979	2.8	275	119	4.0	10.7
	Mar. 1979	3.1				
1978	Mar. 1980	6.6	290	323	4.7	23.4
	Mar. 1980	7.0				
1979	Mar. 1981	3.6	206	400	11.1	17.7

[a]Corrected for drift problems in prototype analog integrator.
[b]Fish near bottom in south end; known underestimates.
[c]Adjusted slightly for anomalous water flow conditions by direct measurement (see Stober et al. 1978).

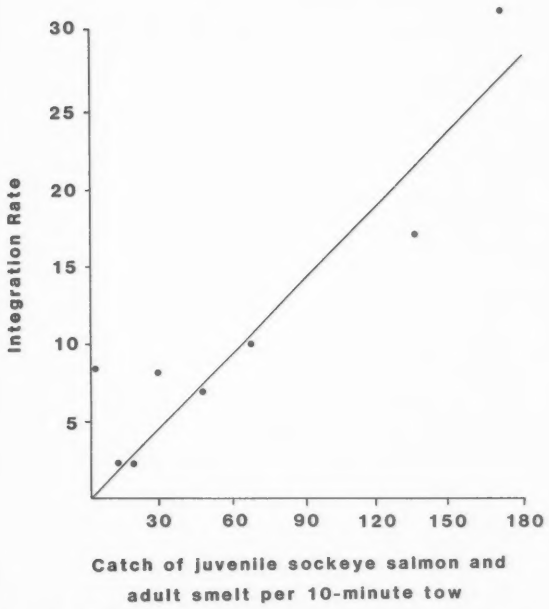

FIG. 1. Comparison of echo integrator output and midwater trawl catches from corresponding depth strata in Lake Washington.

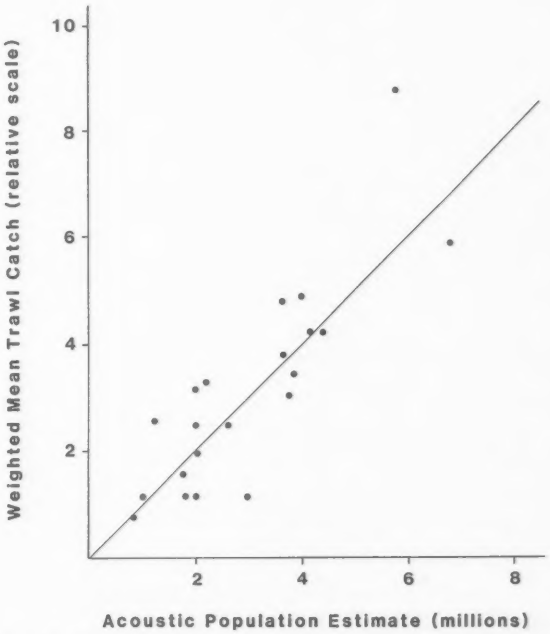

FIG. 2. Comparison of acoustic and midwater trawl estimates of presmolt sockeye salmon, 1970–81.

capacity of the lake. This relationship may also be affected by density-independent factors such as temperature and water flow.

The parent populations for the 13 brood years considered here have ranged from 120 000 to 383 000 fish. Studies of spawning behavior and egg viability suggest that density-dependent mortality associated with limited spawning habitat is not appreciable for these population levels (Stober et al. 1978). Further, there is no indication of density-dependent mortality during lake residence (Bryant 1976). Growth rates in Lake Washington are high, with smolt size at outmigration about 120

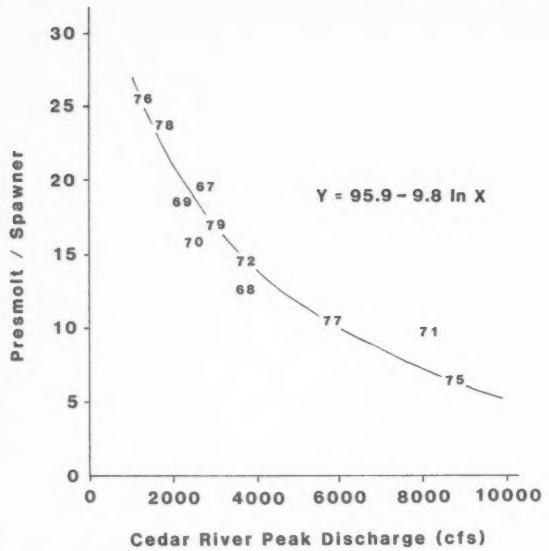

FIG. 3. Cedar River sockeye, flood vs. production, 1967–79. Relationship between annual smolt production and the peak daily discharge from the Cedar River during incubation.

mm and no apparent interaction between population size and weight of smolts. Further, hydroacoustic estimates of abundance during lake residence show very low mortality rates and no suggestion of density-dependent mortality (Bryant 1976). Under these circumstances, one would expect the smolt population to be closely correlated with the size of the spawning population. However, examination of the data in Table 1 shows that the number of smolts produced per spawner varies substantially.

If the acoustic estimates of smolt outmigration are accurate, the poor correlation between smolt abundance and their parent population could only be explained by a major density-independent source of mortality. One potential source would be egg mortality caused by high water flow conditions. High water flows have been suggested as a major cause of egg mortality in other freshwater systems (McNeil 1966, 1969). However, the effects of flooding are generally difficult to isolate because spawning in most systems takes place in several different streams and rivers and over considerable range, so that the impact of local flooding is diffused in the population as a whole. Lake Washington is atypical in that 90% of the spawning takes place in a relatively limited range of a single river. Thus, the population is potentially vulnerable to damage from high water flows in that area. Studies by Stober et al. (1978) over a 2-yr period suggested that flooding in the Cedar River was a major factor in sockeye salmon reproductive success. The long-term hydroacoustic data base allows a more complete evaluation of the relative influence of flooding on the overall sockeye production. For this evaluation, the ratio of the number of smolts (from the hydroacoustic estimates) to the number of spawners was examined as a function of the peak daily water flows in the Cedar River for the in-gravel period (data for USGS hydrographic station near the mouth of the Cedar River). A negative exponential fit to the data produced an r^2 value of 0.94 (Fig. 3). The results strongly indicate that short-term, high-river flows are a dominant factor in the survival to presmolt in this system. Further, the results indirectly verify the hydroacoustic estimates of presmolt populations, since those estimates are inherent in the data in Fig. 3.

Variability in Marine Survival

Since the evidence cited above, including the net tows and the apparent impact of flooding on the sockeye salmon production, supports the precision of the hydroacoustic estimates of smolt outmigration, it follows that the marine survival for the Lake Washington sockeye salmon stock must indeed vary considerably. Whether the absolute values of 4–20% are accurate is a more difficult question, since the available evidence is only able to validate the acoustic estimates as a relative index. However, other studies have indicated very high accuracy for hydroacoustic techniques as absolute measures of abundance (Jakobsson 1983; Nakken and Ulltang 1983; Nunnallee 1983; Thorne 1979, 1983b; Thorne and Thomas 1984), and the average marine survival estimated for Lake Washington, 9.4%, is very close to the 10% marine survival nominally expected for sockeye salmon (Foerster 1968).

The realization that floods have a major effect on the spawning success in Lake Washington can form the basis for sound management and enhancement decisions. The variable marine survival is a more difficult management problem, since it limits the accuracy of run size predictions until and unless our understanding of the complex processes governing oceanic production is much improved (Wooster 1983). However, the starting point for increased understanding is the firm recognition that a problem exists. As a result of the long-term data set from the hydroacoustic surveys on Lake Washington, that recognition is now achieved, and further increase in our capability for run size prediction will require improved understanding of the processes that affect marine survival.

Acknowledgments

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PERSPECTIVES

Rationalizing the Irrational: A Case Study in User Group Participation in Pacific Salmon Management

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Hilborn, R., and W. Luedke. 1987. Rationalizing the irrational: a case study in user group participation in Pacific salmon management. Can. J. Fish. Aquat. Sci. 44: 1796–1805.

Acrimony between industry and government managers is commonplace in the management of many Pacific salmon fisheries. A case study of the chum salmon (*Oncorhynchus keta*) fisheries in southern British Columbia provides insight into the prevailing distrust between fishermen and managers. A recent attempt to bring planned management into what had often been an irrational and highly political activity is described. A management system called the "clockwork" provides all fishermen an opportunity for greater understanding of the management rationale and greater input into the decision-making process. The results of this attempt and implications for achieving management goals are discussed.

La controverse est chose courante entre les gestionnaires de l'industrie et du gouvernement quand il s'agit de gérer bon nombre de pêches du saumon du Pacifique. Une étude type de la pêche du saumon kéta (*Oncorhynchus keta*) dans les eaux du sud de la Colombie-Britannique donne un aperçu de la méfiance qui règne entre les pêcheurs et les gestionnaires. On décrit une tentative récente d'application d'un système de gestion planifiée à cette activité qui s'est souvent révélée irrationnelle et très politisée. Le système de gestion «clockwork» donne à tous les pêcheurs la possibilité de mieux comprendre la logique de la gestion et de participer plus activement à la prise de décisions. On traite des résultats de cette tentative d'application du système et de ses conséquences sur l'atteinte des objectifs de gestion.

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A recurring theme in natural resource management (Walker 1973; Odum and Skjei 1974; Shabman 1974; Cushing 1974; Miller 1976; Wright 1981; Pringle 1985) is that successful management requires cooperation of the user groups. Unfortunately, acrimony is often more prevalent in natural resource management than cooperation, and it is not apparent how more cooperation can be attained. Some suggest that the users should have a dominant role in the management process. Some suggest that cooperation will follow proper scientific management, which requires the manager to have the resource as the primary client and not be influenced by lobbying from the users. Others suggest, and it has been our experience, that cooperation can be attained if users are provided a better understanding of the management system and some involvement in both the short-term decision-making process and the determination of long-term objectives. We present a case study of the formulation and implementation of a management system based on scientific principles but allowing user involvement. This case study provides unique insight into typical problems which hinder success in the management of many natural resources.

The management of Pacific salmon can be an extraordinarily acrimonious process. And as Crutchfield and Pontecorvo (1969) and Wright (1981) pointed out, regulation of the large and efficient net fleets in Alaska, British Columbia, Washington, and Oregon can be particularly troublesome. This is reflected in the Canadian Department of Fisheries and Oceans (DFO) annual operating budget for salmon management of approximately 32% of the landed value of the resource (Pearse 1982).

The acrimony associated with management of the net fisheries can be attributed in part to the large number of decisions that must be made, decisions that may directly affect the livelihoods of thousands of fishermen and related workers. Contrast the many daily decisions on timing and boundaries of salmon fisheries with the once per year decisions of total allowable catches in the management of many groundfish, halibut, or herring stocks in British Columbia and the many opportunities for dispute become clear. The large natural variability in production, timing, and migration of salmon stocks provides further opportunity for dispute. Despite all the money spent on salmon research and management, many in-season net fishery decisions are made with considerable uncertainty. In addition, conflicts often arise between different interest groups or gear users. Allocation of the catch is a particularly contentious issue. Management decisions often affect the share of the catch different types of fishermen receive, and as a result, fishermen may complain and lobby for more time in the next fishery. Finally, much of the in-season

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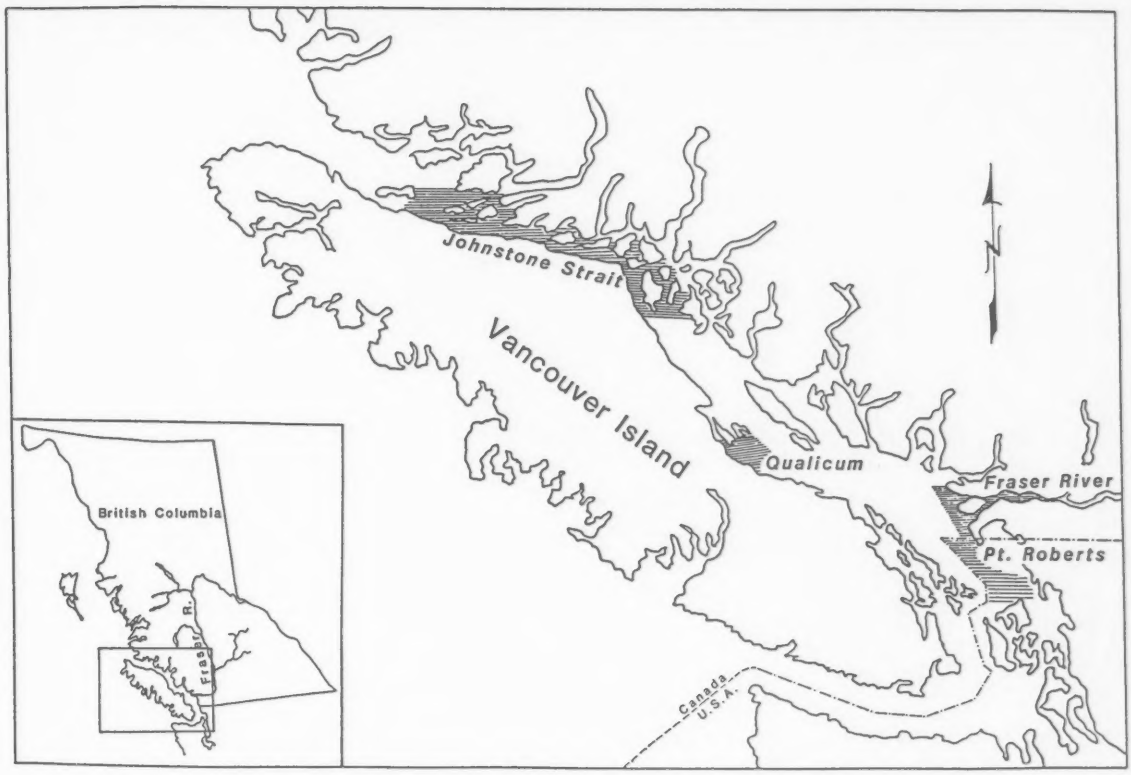

FIG. 1. Major seine and gillnet fisheries (shaded areas) for Study Area chum stocks.

acrimony may result from the paternalistic tradition in salmon management of the strong government agency regulating the fishery in what the government views as the best interest of the fish and the fishermen. This is primarily due to the common property nature of the resource where the fishermen, if left totally unregulated, might fish the stocks to near extinction. But as Pringle (1985) has pointed out, many fishermen are conservation minded and have a legitimate desire to take an active part in the decision-making process. However, until recently, the management process in southern British Columbia has severely limited such participation.

The fishery for chum salmon (*Oncorhynchus keta*) in Johnstone Strait and the Fraser River is an extreme example of conflict over in-season management decisions. Fishermen have occupied DFO offices, bomb threats have been made against employees, and the Minister of Fisheries and Oceans has paid personal attention to day-to-day decisions. Management actions have often resulted from political lobbying by fishermen. It is apparent that acrimony and the resulting lack of cooperation have been a major hindrance to the success of management in this fishery. It is also apparent that the management process must be accepted by the fishermen if it is to succeed. To this end an attempt has been made to change what had been an irrational annual battle between fishermen and government managers into a rationally planned management system in which the fishermen play a significant role. In the following pages we set out the nature of the fishery, the politics of the fishery, what has been attempted, what actually happened, and what was learned.

The Fishery

The region from Johnstone Strait to the Fraser River (Fig. 1), including all tributaries, is called the Study Area in terms of DFO chum management. After an oceanic migration of 3–5 yr, chum salmon return, mainly through Johnstone Strait (Anderson and Beacham 1983), to spawn in these tributaries. The chum salmon are then exploited by three major Canadian and one American fishery (Fig. 1) during a 4- to 6-wk period each fall.

The first in this gauntlet of fisheries, and the largest (Fig. 2), is the Johnstone Strait fishery. Both gillnet and purse-seine boats fish here, but in recent years, seine catches have predominated. The purse seine fleet traditionally consisted of vessels out of local communities such as Port Hardy, Alert Bay, Sointula, and Campbell River, but in the past few years almost every seine boat in British Columbia has fished for chum in Johnstone Strait. This trend of increasing mobility reflects the fishermen's need to extend their individual fishing seasons as capital investment increases and fishing time at each fishery decreases.

Other major Canadian fisheries include a gillnet fishery in the Fraser River and a fishery at Qualicum. The Fraser River fishery harvests only Fraser River stocks, in contrast with the Johnstone Strait fishery which harvests stocks from the entire Study Area. The Qualicum fishery has recently developed to harvest the surplus chum salmon production from hatcheries and spawning channels in the area. While this new fishery originally occurred

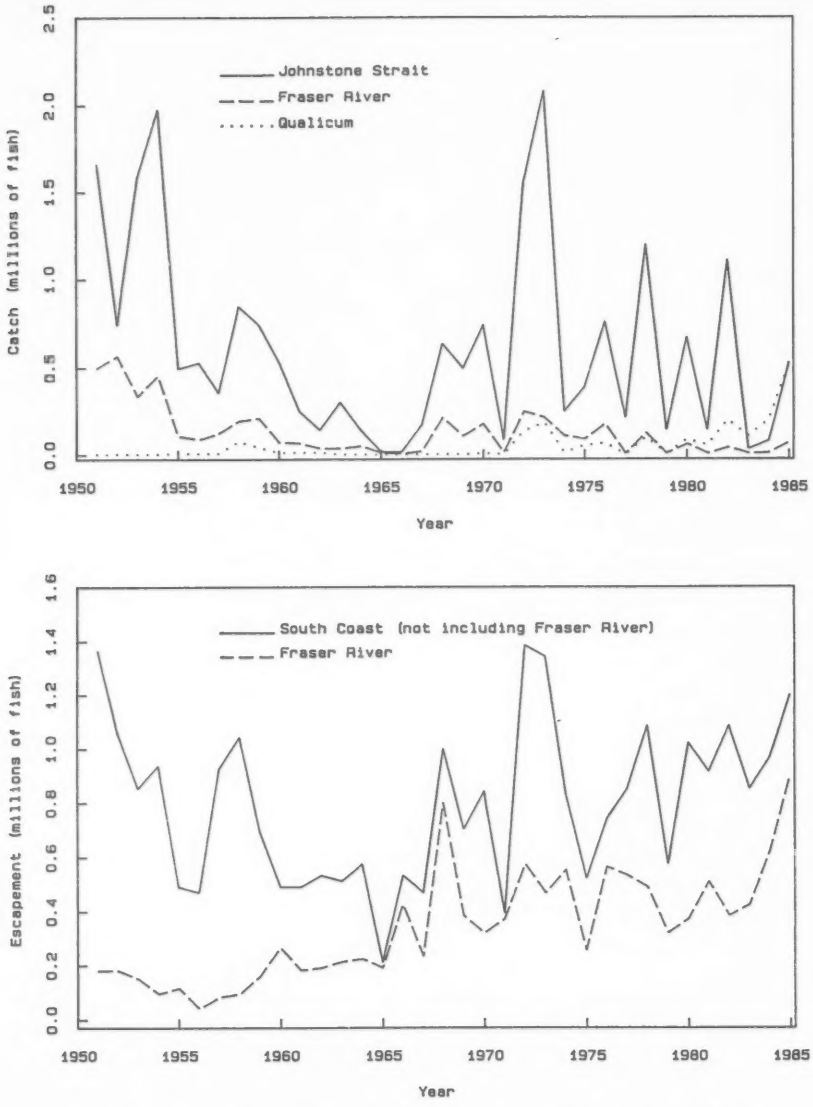

FIG. 2. Historic catch and escapement of chum salmon in major British Columbia fisheries.

in late November, after the hatcheries had taken their brood stock, large surpluses combined with poor prices for the low-quality fish have led to an earlier Qualicum fishery in October. This fishery was originally developed for gill nets only but has opened to both gear types in past years.

There is also an American fishery near the mouth of the Fraser River at Point Roberts which harvests mainly Fraser River chum salmon. As a result, there is a recent tradition of an American fishery at Point Roberts only when there is a chum fishery in Johnstone Strait or the Fraser River.

A major element in the management of chum salmon is the difference in quality and price between the various fisheries. The value of chum salmon (based on appearance and flesh quality) decreases rapidly as it approaches its natal stream. A fish caught in Johnstone Strait in mid-October is called a silver bright and may be worth $1.20 per pound ($3.20 per kilogram), while a dark chum (often called a gumboot) captured in the Fraser River or at Qualicum in November might be worth only $0.30 per pound ($0.80 per kilogram).

Other aspects of chum salmon biology must be considered. While runs of other salmon species are generally dominated by relatively few but productive stocks, the Study Area chum salmon run consists of many smaller stocks. Consequently, mixed-stock fishery concerns, such as protection of smaller stocks, further complicate the management of chum salmon. Another important aspect is that chum salmon are generally the least productive salmon in British Columbia. The average ratio of adult returns per spawner is only 1.5:1, lower than pink

salmon (*O. gorbuscha*) which return at a rate of about 2:1, coho (*O. kisutch*) at 3:1, and sockeye (*O. nerka*) and chinook (*O. tshawytscha*) at 4:1. A result of this generally low rate of return and the natural variation associated with it is that returns are often no greater than the parental brood stock. This has necessitated greatly reduced fishing in many years in an attempt to maintain escapements.

Institutional Structure

Two major groups need to be analysed to understand the bureaucratic nature of chum management. They are DFO and the user groups. Figure 3 presents the organization of DFO as it relates to chum management in southern British Columbia at the time of this study. Note that although both the South Coast and Fraser River divisions are responsible for chum management, the increasing importance of the Johnstone Strait and Qualicum fisheries, along with current depressed level of Fraser River stocks, has given the South Coast Division most of the management responsibility for Study Area chum. The Fraser River Division staff, however, continue to play an active advisory role.

Management actions are implemented by a small army of about 130 fisheries officers with vessel support. They open and close fisheries, patrol fishing boundaries, estimate the catch, collect fish sales records, count escapement, and generally do most of the field work associated with fisheries management. The Johnstone Strait fishery officers are coordinated by the District Supervisor in Campbell River. Local fishermen often voice their concerns about the fishery and the stocks to the District Supervisor, who has direct input into local management plans. The profile of the District Supervisor in Campbell River has increased in the last 10 yr with the importance of the Johnstone Strait fishery.

The District Supervisor reports to the Area Manager. There is one Area Manager in each of the three main divisions of Pacific Region. The South Coast Area Manager, for example, has jurisdiction over all fisheries south of the northern tip of Vancouver Island with the exception of the Fraser River. Each Area Manager has a management staff, consisting of a Senior Management Biologist and a number of other biologists, responsible for specific fisheries. The biologists determine escapement goals and propose fishing patterns and regulations to meet these goals. Their role in chum management has increased since the mid-1970's when the local fisheries officer had most of the management responsibility.

These people are the most active in managing the chum salmon. DFO personnel above the Area Manager are not usually active in the management process, although the Director General, who is the senior DFO official in British Columbia, or the Minister of Fisheries and Oceans in Ottawa may be called in to settle disputes or make recommendations. Fishermen's groups often lobby the minister to supersede decisions made by managers with more socially acceptable decisions.

The major identifiable interest groups which have been important in chum management range from large, well-organized union groups to smaller groups representing communities or specific interests (Table 1). The United Fishermen and Allied Workers Union is the largest such group in British Columbia with several thousand members who represent all gear types (seine, gill net, and troll) as well as shore workers and people on collector boats (called packers). Less formal organizations such as the Concerned Area 13 Salmon Fishermen are formed to provide a unified voice for communities or groups of fishermen. The Fisheries Association of British Columbia represents the processing sector of industry.

For several years, DFO has determined fishing patterns and regulations for chum fisheries after informal consultation with representatives of various fishing communities sitting on the Johnstone Strait – Fraser River Chum Advisory Committee. This is an unofficial body with no formal organization, rules of procedure, or membership, but which has met regularly with DFO since 1976.

Structure of the Management System

The Johnstone Strait – Fraser River chum fishery has been the focus of biological study for over 20 yr (Wickett 1958; Palmer 1972; Anderson 1977; Beacham and Starr 1982; Anderson and Beacham 1983). In this time a management system based on a fixed escapement strategy has evolved for the Study Area chum stocks that is similar to that used for major salmon net fisheries in British Columbia, Washington, and Alaska. The traditional management sequence has been to state the escapement goals for the Fraser and non-Fraser components of the run before the fishing season, assess the runs as they develop in-season, and then allow commercial fisheries to harvest any expected surplus (the amount in excess of the escapement goal).

The size of the Study Area chum salmon return is assessed by three methods. The first method is a preseason forecast based largely on a correlation between pink salmon and chum salmon rates of return for the same brood year. The second method and first in-season indicator is a correlation between total chum run size and chum catch in the first 3 wk of September. The chum run through Johnstone Strait begins in early September, overlapping with the end of late pink or sockeye runs. Early returning chums may then be incidentally caught in major pink or sockeye fisheries, or if no pink or sockeye fisheries are scheduled, a brief opening directed at chum may be used. The third method of estimating total chum return is based on a correlation between total run size and the weekly results of a test fishery for chum salmon conducted in upper Johnstone Strait since 1965.

Based on an average of available estimates, commercial fisheries are opened in Johnstone Strait to harvest any estimated surplus. If the return is particularly large, as many as four 2-d fisheries may be permitted in Johnstone Strait, as well as fisheries in the Fraser River. If a small surplus is expected, one or two openings may be held in Johnstone Strait after the first week of October. Fisheries at this time are thought to target on the enhanced Vancouver Island stocks and have the least impact on the Fraser River stocks. If the run looks to be less than the escapement goal, then no commercial fishery is allowed.

This methodology might well serve as a logical, rational, biologically oriented management system. And in years of extremely good or extremely poor runs, we have observed management to proceed in such a straightforward manner. But when the run size is borderline, and no or few fisheries are planned, this methodology breaks down. Verbal skirmishes between factions of fishermen and between fishermen and DFO become common as the fishermen try to get more fishing time.

Emergence of the Clockwork

We first became aware of the contentious nature of this management process in the fall of 1982. In-season estimates

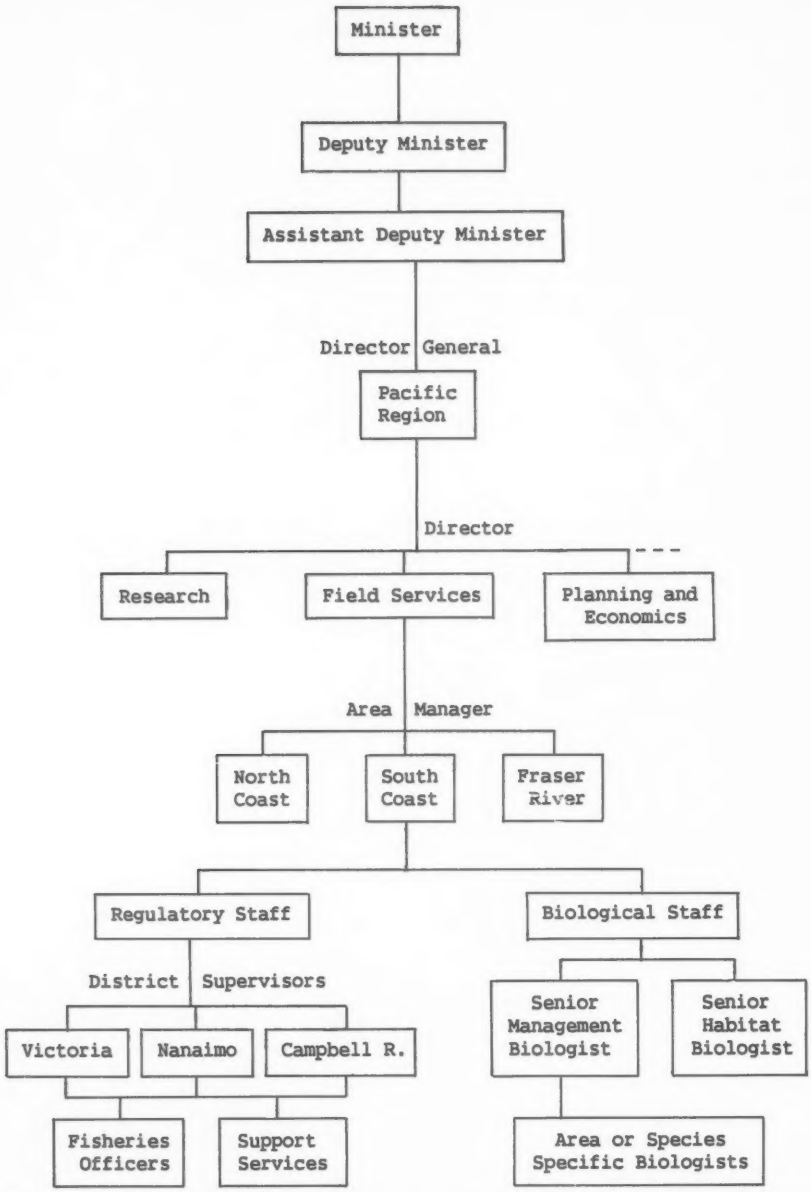

FIG. 3. Organizational structure of DFO as related to chum salmon management in southern British Columbia.

indicated a fishable total run size, but stock identification studies indicated that the Fraser River component was weak, below the escapement goal of 700 000. For this reason DFO managers wanted to stop fishing. Fishermen were seeing a large run pass the fishery and complained bitterly that DFO was "moving the goal posts" when it increased the escapement goal from 500 000 in the previous year. They successfully lobbied for more fishing time.

After the season a general feeling of discontent over the management of the fishery was apparent within industry as well as government. Some members of the Johnstone Strait – Fraser River Chum Advisory Committee approached us with their concerns and asked us to review the current management system. Our impression was that the system could be rationalized into a simpler and more generally acceptable form. We worked with industry to initiate a scheme to rationalize the decision-making process and provide increased participation of industry. The "clockwork," as it was called, would require DFO managers and fishermen's representatives to collectively formulate a set of rules by which the fishery would be managed.

This would have to be completed before the fishing season. The in-season decision-making process would then run like a wound clock; fisheries would open and close according to these rules. We also felt it was important to publish the rules in such a way that any commercial fisherman would be able to calculate the size of the chum run, the allowable catch, and the number of days' fishing that could be expected.

The purpose of codifying the rules would be to eliminate the in-season wrangling between fishermen and DFO, when an extra day of fishing could mean thousands of dollars to each fisherman. The clockwork would be formulated when more objective thought prevailed, before the season. If both sides could abide by the rules during the season, a new sense of cooperation might be possible.

The groundwork for the clockwork already existed; the Johnstone Strait – Fraser River Chum Advisory Committee met regularly with DFO and was generally accepted within the fishing industry as a useful form of interaction with DFO. In addition the in-season estimation methods of run size methods were well developed and were simple enough to be formalized in a form everyone could understand. With DFO and industry support for the clockwork concept, we were invited to become technical advisors to industry and agreed to help formulate the clockwork.

Implementation History

Implementation of the clockwork proceeded through the Johnstone Strait – Fraser River Chum Advisory Committee and DFO. A trial period of 3 yr was designated during which the clockwork could be implemented and refined into an acceptable management system. With the in-season stock assessment methods in place, it initially appeared that the only major requirement would be agreement to a set of rules. It soon became clear, however, that implementation would require much more time, as many stumbling blocks relating to the prevailing distrust between industry and government, and the difficulty of changing a traditional management system, would have to be overcome. In the following pages we outline our experience with the committee and the advisory process during this 3-yr period. We also describe the events surrounding the implementation of the clockwork in the Johnstone Strait chum fishery.

The First Year (1983)

We first introduced the clockwork concept to the committee in June of 1983 at a meeting where DFO presented expectations of a poor return for the coming season with no commercial fishing except at Qualicum, a terminal fishery for enhanced stocks. The advisors generally agreed that conservation measures were necessary. The advisors also agreed that the clockwork concept could be useful in the Johnstone Strait chum fishery, and were willing to put something in place for the 1983 season.

Our first task was to evaluate the in-season run size estimation methods, which would be the basis of the clockwork rules. We assumed that the advisors would more readily accept the proposed rules if we found the statistics and analyses acceptable. The clockwork concept required that all rules be simple and clearly stated. So we first recommended a simplification of the in-season management methods, especially the run size estimate from the third week of September catch. Although six estimates from six correlations between run size and catch were available, only one should be used in the clockwork.

TABLE 1. Fishermen's organizations in southern British Columbia.

Organization	Membership
United Fishermen and Allied Workers Union (UFAWU)	6000
Native Brotherhood of British Columbia	1200
Vessel Owners Association of British Columbia	200
Pacific Trollers Association	350
Pacific Gill Netters Association	120
Gulf Trollers Association	50
Sport Fish Advisory Board	<50
Concerned Area 13 Fishermen	<50
Johnstone Strait Area Fishermen	<50
Port Hardy Seiners	<50
Fisheries Association of British Columbia	<50

We also felt the clockwork required rules for all the related fisheries. A clear statement of management rules for Fraser River as well as non-Fraser stocks would have to be included. As it stood, if the run of any stock was smaller than its escapement goal, then there would be no fishery in Johnstone Strait; only terminal fisheries were possible. This meant that the non-Fraser portion of the run could be very strong, but if the Fraser were less than 700 000 there would be no fishery. This obviously could lead to dispute (e.g. 1982), since maximization of yield from a mixed-stock fishery may result in some of the stocks not reaching their escapement target.

In September of 1983, before the chum season, DFO presented some basic rules and their escapement objectives. The advisors accepted our assessment and generally agreed to the clockwork rules (i.e. no fishing this year). We saw it as a modest beginning that was sufficient for a year in which no chum fishery would likely take place in Johnstone Strait.

The 1983 fishery

At no time during September and October was there any indication of a fishable stock. The clockwork consequently was not really tested in 1983. With the advisors' acceptance of no fishery in Johnstone Strait or the Fraser River, attention turned to the terminal fishery at Qualicum. Prior to 1982 this fishery had been held in late November or early December, only after the required escapement for the hatchery had been achieved. As a consequence, the quality of the catch was extremely poor, the processing companies expressed little desire to buy the catch, and fishermen received little return.

In order to provide a better quality catch, the management strategy was altered to allow a fishery on a portion of the anticipated surplus in October. There was a risk that the hatchery might not achieve sufficient brood stock, but based on the size of previous returns and the much higher quality of fish in the earlier opening, it was felt to be worth the risk. Some advisors were concerned that an early fishery could intercept significant numbers of non-Qualicum stocks, particularly Fraser River chums migrating through the area. Regardless, the fishery took place, although the catch was sampled to determine stock composition using an identification technique based on biochemical electrophoresis. The samples indicated the presence of Fraser River and United States fish, approaching 25% Fraser fish alone in the area farthest offshore. The fishery was not the terminal fishery DFO claimed it would be; future

management strategies would have to reduce the incidental catch of Fraser River and United States bound fish.

Assessment of the 1983 season

After the season, we felt we had made a modest beginning with the clockwork and had been fortunate that there was little controversy over the size of the run; the preseason forecast, September estimate from commercial catches, and October test fishing estimates all indicated similar stock sizes. In addition, the Qualicum fishery was considered a commercial success because quality and prices were good, and the hatchery met its requirements. We recognized, however, that changes in the clockwork were required before the next fishing season. The clockwork still lacked a crucial component: some clearly stated objectives determined by all user groups. In addition, rules for the Johnstone Strait, Fraser River, and Qualicum fisheries would have to be included in a clearly stated format.

The Second Year (1984)

We initiated these changes through a workshop with DFO and the advisors in April of 1984 at the University of British Columbia. Objectives of the chum fishery were established and some alternative fishing strategies to meet the objectives were introduced and analysed. The overall objective expressed by the Johnstone Strait – Fraser River Chum Advisors was (1) to achieve the maximum potential of the resource and maximum long-term benefits to the fishermen. In addition the following objectives were established: (2) define the optimum escapement goal as 2 500 000 wild chum for the Study Area, including an escapement goal of 700 000 for the Fraser River, (3) reach this escapement goal within three cycles (12–15 yr), (4) learn as much as possible about the productivity of the stocks, (5) allow limited fishing at low stock sizes, and (6) stabilize the annual catch. During the workshop many advisors expressed concern over the uncertainty about the optimal escapement goals, especially since the goal for the Study Area as a whole had not been reached in the last 20 yr, and only once in the Fraser River. The advisors suggested that any immediate attempt to reach this level would produce too much hardship on the fishermen. Furthermore, it was generally agreed that it would not be disastrous to continue with lower than optimal escapements. Consequently a lesser goal was established for the years 1984–86, based on achieving above-average returns. An escapement of 1 800 000 wild chum would be required for the Study Area, 500 000 of these in the Fraser River. It was important to define these goals for wild stocks only, since the proportion of enhanced fish in the total run would increase over the next few years.

With these objectives in mind, alternative harvesting strategies were discussed, including a constant harvest rate (with rates of 20, 30, or 40%), fixed escapement, and a variable harvest rate strategy which allowed harvesting at 10, 20, 30, or 40% depending on the size of the run. There was general agreement that a ceiling on the harvest rate of 40% during very good years was desirable to allow large escapements and provide information about the productivity of the stocks. However, there was considerable disagreement about what to do in poor years. Fraser River fishermen were generally concerned about poor escapements and the long time needed to rebuild the stocks under the constant harvest rate alternatives. Many Johnstone Strait area fishermen, however, were more concerned about the financial wellbeing of the fishermen in their area, indicating the importance of even one opening in a poor year. This precluded the continued use of a fixed escapement strategy which would require several years with no fishing to meet the escapement objectives. Eventually a variable or stepped harvest rate strategy was adopted (see Table 2) and called the "Advisors' plan." The minimum total stock of 2.6 million before commercial fishing was allowed included 1.8 million wild chum, 700 000 "enhanced" chum, and 100 000 "American" chum.

TABLE 2. The Advisors' Plan to determine harvest of chum salmon in Johnstone Strait.

Total stock size (millions)	Allowable harvest rate (%)	Probable number of openings
0–2.6	10[a]	0
2.6–3.2	20	1–2
3.2–4.8	30	2–3
4.8 up	40	4 or more

[a]3–10% of the total run is caught in test fisheries, native fisheries, and early commercial fisheries.

Objectives and fishing patterns for the Qualicum fishery were also discussed. Since the preseason forecast once again suggested that no fishery would take place in Johnstone Strait, the Qualicum fishery again became an important component of the fishing season. In response to the high incidental catch of Fraser River chum the previous year, DFO proposed closing the areas of the fishery where the incidence of Fraser River chum had been high. This would be accomplished by electrophoretic determination of the stock composition before any fishery was opened. Furthermore, a fishery would take place only if the Fraser River component in the remaining area was less than 10% of the total.

The proposed rules of the Johnstone Strait and Qualicum fisheries were documented by DFO and were to be presented to the Johnstone Strait – Fraser River Advisors before the start of the chum fishery.

The 1984 fishery

With many salmon stocks at low levels, 1984 was a poor year for most British Columbia fishermen. This resulted in special significance for the fall chum fishery in Johnstone Strait. The prevailing attitude of fishermen, as the chum season began, was that this was their last chance to salvage the season.

On this note, the first advisory meeting of the chum season was held on September 21. The first in-season estimate of run strength, using the third week of September chum catch, indicated a total run size of 1.4 million, far below the level required by the rules for a commercial fishery in Johnstone Strait. In keeping with the clockwork, no fishery could be allowed, unless upcoming test fishing results indicated a much larger run size.

The response of the advisors was mixed. While some advisors thought the run was too small to fish, several Johnstone Strait area representatives disputed the results of the first in-season run size estimate. They suggested that the small catch in the third week of September fishery was due to the timing of the fishery: early in the week instead of late, and during a moderate tide (catches are generally larger when tidal differences are great). These fishermen also suggested that the run may be late because of residual El Niño effects. As technical advisors to the fishermen, we expressed our opinion that the first

in-season estimate was likely valid (as the correlation was based on catches from a variety of times and tides) and even substantial increases in the catch would not have indicated a fishable stock size. The majority of the advisors agreed that there should be no fishery, as outlined by the clockwork, until the next in-season stock size estimate was available.

The next meeting took place in the first week of October, with more than 50 fishermen in attendance. Although estimates of stock size from the test fishery were again below the minimum required for a commercial fishery, a group of native Johnstone Strait fishermen, with a lawyer as spokesman, continued to press for a Johnstone Strait fishery. They suggested that the test fishery was not being conducted properly; there were reports that the actual catch was greater than that reported and used by DFO and that the test fishing effort was too low. Consequently, a few advisors suggested the run was larger than indicated. DFO cited the proven reliability of the test fishery and invited any advisor to observe the test fishery first hand from the test vessel.

The advisors as a whole then introduced a plan which would provide a Johnstone Strait fishery with minimal impact on the Fraser River stocks. Using electrophoretic identification of stocks, they suggested that a fishery should occur when the run consisted of mainly enhanced Qualicum stocks and less than 10% Fraser River stocks. DFO responded that this would not protect other weak stocks, and that in keeping with the clockwork, no fishery would be possible. After a long and heated discussion, DFO also indicated that if a fishery occurred in Johnstone Strait, there would be a fishery at Point Roberts, U.S., which would take a substantial number of Fraser River fish. DFO indicated that as long as we did not fish in Johnstone Strait the Americans would not fish at Point Roberts. The fishermen felt bitter that this had not been indicated earlier and suggested that DFO should confirm this American approach before any final decision was made. The meeting soon broke up, with another meeting scheduled for the next week in the Johnstone Strait region.

There was a further appeal by local fishermen for a Johnstone Strait fishery at this regional meeting; however, with the test fishing still indicating a very weak stock and the Americans indicating they would like to hold a fishery at Point Roberts, many other advisors agreed that no fishery should be allowed in Johnstone Strait, as outlined in the clockwork. Subsequently, much criticism was directed at DFO on the way the salmon fisheries were managed in 1984, including the lack of concern for the fishermen's livelihoods and the way the advisory process and clockwork scheme were proceeding.

With general agreement that no fishery should be allowed in Johnstone Strait, the focus of attention shifted to the terminal fishery at Qualicum. This fishery proceeded with no major problems, the incidental catch of Fraser River stocks was reduced to below 3%, and although the catch per boat was low, it was regarded as a successful fishery.

Assessment of the 1984 season

The poor 1984 fishing season provided a dramatic test of the clockwork approach to management of the Johnstone Strait chum fishery. Despite great pressure for a fishery the clockwork was successful. At the most superficial level all management decisions during the season were consistent with the clockwork rules; a large portion of the small run reached the spawning areas. Although both industry and government reaffirmed their commitment to the advisory process and the clockwork, many problems were identified, not the least of which was the continued in-season acrimony between fishermen and managers.

The most pressing problem was the lack of a formalized advisory process. Changing membership and intrusion of special interest groups through the season resulted in many delays and disputes. The advisors generally agreed that a more formalized structure and procedure, with a set membership, voting, and minutes, would lend the process much more credibility.

Improving the presentation of the clockwork was also necessary. The presentation by DFO was often confusing and inconsistent from year to year and week to week. A simplified, consistent, and professional approach to presenting the rules, background documents, options, etc., would produce a better working relationship between fishermen and managers. It was also necessary to produce complete documentation of the clockwork, with information on the purpose of the clockwork, as well as procedure, background, and rules. General distribution of this document to all fishermen would provide a better general knowledge and understanding of chum management.

The Third Year (1985)

1985 was a very successful year for most British Columbia fishermen. Large sockeye (*O. nerka*) and pink salmon (*O. gorbuscha*) returns produced greater than average fishing time and catches. Consequently the mood among most fishermen appeared to be conciliatory as the chum salmon season approached. The total chum return was expected to be at a fishable level of approximately 2.8 million, producing anticipation among fishermen of continued good fishing.

One of our main objectives this year was to provide the advisors with a written set of rules and a simple guide to allow fishermen first-hand experience with in-season stock assessment. With their feedback and approval, such a document would be distributed to all fishermen in future years.

Another objective was to resolve the continual conflict over the test fishing methodology in Johnstone Strait. Each year, fishermen complained that the test fishery was not producing a representative indication of the size of the run, citing problems such as nonrandom distribution of effort within the test fishing area. A statistical analysis of the test fishery by one of us (as technical advisor to industry) and subsequent discussion with DFO and the local Johnstone Strait advisors resulted in the initiation of an additional test fishery with a more systematic sampling design. This new test fishery would not provide usable information on the short term, but would build a data base that might provide an alternative run size indicator to the original test fishery.

Finally, formalization of the advisory process was generally regarded as a necessary objective by all participants. However, renewed emphasis by DFO to provide user input into fisheries management resulted in an expansion of the process to include other areas and other species of salmon. This resulted in a larger committee to accommodate the expanded interest and a step backwards in the formalization of the advisory process. Late in the season the South Coast Area Manager initiated a move to formalize the membership of the committee for the 1986 season.

The 1985 fishery

A fishable stock of 2.9 million chum was estimated from the in-season stock size indicators. In consultation with the advisors, a 1-d fishery was planned for the Johnstone Strait area in the second week of October. The chum salmon catch during this

fishery was very large, approximately 13% of the total run, precluding the possibility of another fishery (under the Advisors Plan the total catch should not exceed 20% including catch in earlier salmon fisheries, test fisheries, and native food fisheries). However, some local residents of the Johnstone Strait area suggested that the run was much larger than DFO estimated from the old test fishery. They based their assessment on large catches in the new test fishery and in the native food fishery. In keeping with the clockwork, these fishermen were unsuccessful in their lobbying to achieve another opening in Johnstone Strait.

The focus of attention then shifted to the Fraser River and differing interpretation of the clockwork rules. The allowable catch of chum had already been achieved in the 1-d fishery in Johnstone Strait, the noncommercial fisheries, and in incidental catch in other fisheries. There was some dispute as to whether the chum catch in an earlier Fraser River fishery for pink salmon should be included as incidental catch or a chum fishery. Consequently, it was not clear that a fishery would be allowed in the Fraser River. Fraser River fishermen suggested that they were guaranteed a chum fishery under the clockwork in response to the Johnstone Strait fishery. When an American fishery was held at Point Roberts, the desire of the Fraser River fishermen to be allowed a fishery intensified. In late November, a 1-d chum fishery was held in the Fraser River; however, poor weather conditions and a sharp decline in the number of fish entering the system resulted in a small catch.

Finally, attention focused on the terminal fishery at Qualicum where a large return was expected. An earlier fishery in mid-October was generally regarded as successful with the good quality of chum being caught. However, in November, several additional fisheries were planned to catch the surplus not required by the hatchery. The market for the low-quality chum caught during these fisheries was poor, resulting in low prices to fishermen and difficulty in selling the catch. The situation was thought to be indicative of future seasons when even larger returns to the hatchery were expected.

Assessment of the 1985 season

In contrast with the poor season preceding the chum fishery in 1984, the salmon fisheries preceding the chum fishery in 1985 were very successful. Regardless, the view of some fishermen that the chum return was larger than estimated, and ambiguity in the rules for managing the different fisheries, resulted in fishermen lobbying for more fishing time. Despite these problems the clockwork was largely successful; harvest rates did not exceed those determined by the clockwork. The Fraser River escapement of chum salmon was the highest on record at 900 000 out of a total Fraser River run estimated at 1.27 million. Furthermore, industry and government cooperation in the design of a new test fishery in Upper Johnstone Strait indicated the merits of co-management.

Certainly the identified problems would have to be resolved. The committee still required a more formal structure and process. Moreover, rather than just a set of rules for each fishery in the clockwork, it appeared that a clockwork specific to each fishery, but still within the context of the overall strategy for the mixed-stock fishery in Johnstone Strait, would provide better management. The advisors generally approved of our efforts to distribute a clockwork guide to all fishermen, with the goal that fishermen outside the committee should know more about the management system.

Discussion

During 1983–85 the clockwork proved to be a useful management tool. At its most superficial level the clockwork has ensured that management decisions taken have been consistent with rules developed by industry and government. This would ensure a rebuilding of the chum stocks and increased fishing in the future. The clockwork has also provided a forum in which management strategies and in-season fishing plans can be determined and discussed. This forum has provided an opportunity for DFO to learn from industry's experience and vice versa. Unfortunately the clockwork has only been partially successful in alleviating the acrimony associated with the in-season management of the Johnstone Strait and Fraser River fisheries.

This acrimony may always exist, for when fishermen's livelihoods are adversely affected by management decisions, they will fight. But some of the acrimony may be more entrenched than just the fleet's success in fisheries prior to the chum fishery. The majority of the dissident Johnstone Strait fishermen are natives who see their traditional fishing patterns and locations being disrupted. Many perceive developments such as the Qualicum fishery as a threat to their traditional fishing patterns. This often has pitted them against other mostly non-native fishermen of the Johnstone Strait area who have generally supported development of the Qualicum fishery and controversial conservation measures.

Furthermore, the standard argument for conservation of renewable resources "if you take less now you will have more in the future" may not be true for the specific interests of those Johnstone Strait fishermen who are not willing to move to other fisheries. Chum salmon are not very productive, producing on average only 1.5 adults per spawner in 3 or 4 yr. This represents an annual rate of increase between 10 and 15%. This is lower than many fishermen pay on their loans. In addition, the Johnstone Strait fishermen may have to share any future benefits with fishermen in other fisheries. Foregoing 100 000 fish now means on average the run 4 yr from now will be 150 000 fish larger. But these fish may be split among fishermen in Johnstone Strait, the Qualicum area, the Fraser River, and the United States at Point Roberts.

Despite these inherent difficulties the clockwork has proven it can be successful in producing user cooperation in salmon management. During 1983–85, we learned a great deal about the co-management process, what should and should not be done. We identified several elements we feel are necessary for a clockwork type management system to be successful:

(1) An advisory committee representing all user groups, with a formalized structure and procedure, a set membership, minutes, and voting.

(2) A set of objectives formulated by all user groups with the management agency.

(3) The management agency should provide a forum to educate industry, allow discussion, and review clockwork components.

(4) A simple and clearly stated set of rules which will outline management strategies and determine in-season management actions. A separate set of rules, or perhaps separate clockwork, may be necessary for individual fisheries, within the context of the overall strategy.

(5) Complete documentation to provide industry (and especially the advisors) with background, objectives, methods, and rules of the management system. All or part of the documenta-

tion should be widely distributed within industry to provide general background on how the system works and how management decisions will be made.

The clockwork appears to be an important advance in user involvement in salmon management. To our knowledge it is the first opportunity commercial fishermen in British Columbia have had to participate in the setting of fishery goals and determining the rationale of the in-season management decision-making process. The clockwork has gone through an evolution in the first 3 yr. We have corrected mistakes and inadequacies as we were able to identify them. While the whole process will be reviewed and evaluated by industry and management before the next season, we believe that a viable and functioning clockwork will continue to bring the chum fishery back to near historical importance as a major fishery in southern British Columbia.

While these lessons have been learned for a particular, and somewhat unusual, fisheries management situation, we can see immediate application to a great number of fisheries. Almost all salmon net fisheries in the United States and Canada involve some type of in-season management, with some form of user group participation. The general principles outlined above should be applicable to all salmon net fisheries. Other fisheries, particularly salmon troll, bottom fish, and herring fisheries, do not have the detailed in-season run size estimation problem associated with the salmon net fisheries. However, in many cases they still do have the same need for formulation of a harvest strategy and implementation of regulations such as quotas and season lengths. Again the general process and principles should apply.

With wider reference to involving user groups in the decision-making process, we can take some of our experience in the British Columbia chum fishery and use it to cast a series of hypotheses regarding other types of fisheries:

(1) Resource users will cooperate in formulating rules for fisheries management that are in their self interest. In doing this they will work for the best interests of a group, rather than personal self interest. If the rules do not appear to be in their self interest, the users will not participate in a constructive fashion.

(2) To get user cooperation, the process must be credible and verifiable.

(3) Clarity and simplicity facilitate participation in the management process. Ambiguity opens the process to challenge.

(4) Trust is earned over time as people's behaviour matches what they say. There is no shortcut. Only when managers and fishermen do and say the same thing will they accumulate trust that will permit a continuing working relationship.

(5) The biogeography of the resource and resource users must match. If significant actors are not included in the management process, there is great potential for the process to fail due to unexpected actions taken outside of the cooperative management process.

(6) A significant requirement of management is keeping people's expectations reasonable. Management must be careful not to generate expectations that can not be met.

User group participation is a growing aspect of all fisheries, and indeed all resource management. What we have learned in this fishery will, we hope, have wide application.

Acknowledgements

We would like to thank the members of the Johnstone Strait – Fraser River Chum Salmon Advisory Committee for the opportunity to work with them, and the DFO staff for the hours they spent with us. In particular, Dennis Brock, Morley Farwell, Al Gould, Leroy Hopwo, Richard Johnstone, and Ed Safarik Jr. deserve special thanks for their help and comments. Drs. Courtland Smith and Susan Peterson provided extremely helpful comments and review. This work was supported by the British Columbia Science Council.

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Comment on "Seaweeds, Sea Urchins, and Lobsters: A Reappraisal" by R. J. Miller

In his review of interactions among species on the Atlantic coast of Nova Scotia, Miller (1985a) surveyed the history of lobster – sea urchin – kelp studies quite thoroughly. He rejected the hypothesis that predation, especially by American lobsters, controlled the abundance of sea urchins. I will argue that the grounds used to reject the predation hypothesis — the facts, but more importantly the methods — were too weak. Although the predation hypothesis has problems, and there are now several competing explanations for sea urchin – kelp bed interactions, it remains a viable alternative explanation until disproven. I do not consider it disproven.

First, one must recognize that Miller's approach is logically correct. It is not possible to test the lobster predation hypothesis of Mann and Breen (1972) experimentally: the time and spatial scales are too large, and the fishery far too well established, for direct experiments to be practical (Breen and Mann 1976). Nevertheless, this kind of hypothesis could easily be disproven: one needs only to demonstrate from the facts (abundances, feedings rates, selectivities, etc.) that predation by lobsters (or whatever predator specified) is too weak under realistic assumptions and conditions to limit sea urchin densities. Apart from Coleman (1978; see Breen 1980), only Miller has challenged the conclusion of Breen and Mann (1976) with this approach. Instead, criticism of the lobster predation hypothesis has been that it has "not been substantiated" (Vadas et al. 1986) or that "evidence is at present insufficient" to support it (Pringle et al. 1980). Hypotheses can never be "substantiated," nor "sufficient evidence" found to confirm them; instead, science progresses through attempts to falsify and reject hypotheses by demonstrating logical inconsistency with observed fact (Popper 1959).

Miller's review of lobster feeding studies has flaws; consequently the input to his calculations is questionable. First, his review is incomplete — among the missing studies are Squires (1970) and Reddin (1973); the latter study obtained relative prey preferences different from those of Elner (1980). A "reappraisal" should examine the whole body of lobster feeding data. Second, he described my feeding experiments incorrectly and reported the results incorrectly. When five lobsters were offered five prey species two at a time from July to September in underwater cages, the mean rate of feeding on sea urchins (over all prey combinations involving sea urchins) was 2.5% body weight per day, not 0.4% (see Breen 1974, p. 53). This is a sixfold error. When lobsters were offered only sea urchins in both the laboratory and underwater cages, their feeding rate was a function of prey abundance and temperature (Breen 1974, p. 69). From that relation, the feeding rate at 12.5°C and 0.5 kg/m^2 was 13.3% of body weight per day, again greater than the 2–11% in Miller's table 1. Third, he included stomach content studies, which are not very useful in estimating the impact of lobster and crab feeding. Only the hard parts of prey can usually be identified in stomachs (Elner et al. 1985). Lobsters tend not to ingest prey hard parts (Carter and Steele 1982a), and some ingested hard parts have long residence times in the stomach (Carter and Steele 1982b). One could examine lobster stomachs immediately after feeding on known prey; but this has been done only by Carter and Steele (1982b) to examine residence times of hard parts. Even if stomach contents reflect the diet, the diet depends on prey availability, which is rarely measured when stomachs are examined. Again, Carter and Steele (1982b) are the only authors to have measured this; and they neither present the availability data nor follow up on the point. For these reasons I consider the stomach content data to be irrelevant to the issue of lobster feeding impact. As a result of the problems in his table 1, Miller bases his calculations on lobster predation rates of sea urchins which might be too low; thus his estimates may be unrealistically low.

The problem with methodology is more serious. The method must be powerful enough to make a convincing demonstration. Lobster feeding is a complex process influenced by temperature, lobster size, total food availability, selectivity by lobsters for one prey over another, the species composition of available prey, and the relative sizes of lobster and prey. It may also be influenced by switching or complex behavioural interactions. To estimate the impact of a specific lobster density on an assemblage of prey requires a correspondingly detailed calculation: one that begins with precise state specifications, that includes at least the known facts bearing on the interactions just listed, and that describes the dynamics of the prey. No simple serial calculation, such as that used by Miller, can be adequate. A simplified approach perforce excludes most of what is known. The known complexity and the wealth of existing data dictate the use of some kind of model, run in accordance with basic rules to obtain an unbiased result. Such a model must incorporate what is known of those influences on lobster feeding described above. It must begin with careful state specifications, for instance, the densities and size distributions of sea urchins, lobsters, and other prey in the kelp system phase. It must incorporate what is known about the population dynamics of predators and prey involved. All such models are entirely useless at demonstrating that any ecological interaction exists; they are useful only in demonstrating that an outcome of interest is impossible. Such models are capable of demonstrating logical incompatability between hypothesis and fact. While Miller's approach is the correct one, his method is too weak to be convincing.

There is a large and still-increasing body of facts bearing on the dynamics of the Atlantic Nova Scotia coastal ecosystem. There are now four plausible hypothesis groups which explain the dynamics of sea urchins and kelp beds. These are as follows. First, changes in predation pressure could allow sea urchins to increase. So far only wolffish have been credibly eliminated as potentially limiting predators (Breen 1974), but predation hypotheses have some problems. They no longer explain all the facts; they are especially weak in accounting for complex sea urchin behaviour (Bernstein et al. 1981, 1983; Tegner and Levin 1983; Mann 1985) and in explaining the effects of the physical environment on the system (see Dayton and Tegner 1984; Harris et al. 1984; Ebeling et al. 1985). Second, simple changes in sea urchin behaviour might act independently of sea

urchin density but with radical consequences on kelp beds. This hypothesis was developed to account for events in Calfornia kelp beds by Dean et al. (1984) and Harrold and Reed (1985), who suggested that behaviour is strongly influenced by the supply of algal drift. Third, Miller (1985b) and Scheibling (1986) suggested that the well-documented disappearance of kelp from eastern Nova Scotia in the 1970's and the widespread mortality of sea urchins in the 1980's are phases in an abundance and disease cycle. Fourth, sea urchins might increase because their reproductive success is higher under particular hydrographic conditions (Mann 1985), as Foreman (1977) suggested for *Strongylocentrotus droebachiensis* in British Columbia. Other alternative hypotheses may exist, and these major groups may not be mutually exclusive. (However, one must be cautious not to develop hypotheses that explain all imaginable events and are thus untestable.)

We are certainly not back to square one. When faced with more than one hypothesis that explains the facts, one tries to eliminate them all through logical or experimental testing, in that way arriving at a survivor (Popper 1959; Dayton and Oliver 1980). We need rigorous attempts to demonstrate the logical or experimental impossibility of these hypotheses. The various predation hypotheses are especially amenable to logical testing; Vadas et al. (1986) is a good example of experimental rejection. Second, one needs to identify critical differences in the logical predictions and consequences of the alternative explanations, and design experiments to test critical predictions and reject one or more alternatives — Paul A. Breen, *Ministry of Agriculture and Fisheries, Fisheries Research Centre, Box 297, Wellington, New Zealand.* (J8951)

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Reply to Comment by P. A. Breen

Breen disagrees with the data and methods I used to investigate the hypothesis that lobster predation controls sea urchin grazing. I concluded from reviewing a large body of literature that lobsters are unimportant predators of sea urchins, both now and in recent decades. This is still my view.

Breen's first two paragraphs discuss whether various authors considered the hypothesis to be rejected or not supported; his last two paragraphs are a mini-review of factors controlling sea urchin grazing and a discussion of hypothesis testing.

His third paragraph criticises calculations of lobster feeding rates on urchins, and includes his only specific criticisms. These calculations are a small but important part of the Perspective reviewing interactions of seaweed, sea urchins, and sea urchin predators (Miller 1985, p. 2062–2063).

Breen states that my review of lobster feeding studies is incomplete and references Squires (1970) and Reddin (1973)

as evidence Herrick (1895) and Weiss (1970) could have been added to the omissions. Squires and Weiss were omitted because their stomach content data were presented as frequency of occurrence rather than weight or volume of prey types. The latter units were needed for calculating gram of urchin eaten per gram lobster per year. However, for those interested, Squires found urchin remains in 4% of the stomachs examined, and Weiss did not mention urchins as occurring. Herrick put echinoderms near the bottom of a list of prey groups presented "in order of relative abundance" and gave sea urchin parts as "rare." I was unable to evaluate prey preference data in a thesis by Reddin because the experimental conditions of prey abundance, prey size, and lobster size were not included, and presentation of some of the results was unclear. Prey size, predator size, and relative abundance of prey choices are known to affect prey selection (Evans and Mann 1977; Elner 1980; Carter and Steele 1982a).

In the most recent study of lobster stomach contents, Elner and Campbell (1987) presented data for 917 lobsters collected from urchin-dominated barrens and, for the first time, 115 lobster collected from a macroalgal bed where urchins were rare. The volume of urchins in the stomach contents was only 5% for the barrens and 0.04% for the algal bed.

Contrary to a statement by Breen, lobsters do ingest hard parts of urchins (Carter and Steele 1982a; L. V. Colpitts and R. W. Elner, St. Andrews Biological Station, St. Andrews, N.B. E0G 2X0, unpubl.) as referenced in table 1 of the Perspective. Also, the weight of urchins in lobster stomachs was multiplied by 3 to account for the uningested portion. If urchin hard parts have a longer than average residence time in the lobster stomach as Breen implied (this idea was not supported by Carter and Steele 1982b), then my calculation of urchin importance in the lobster diet should be even lower.

Breen correctly states that Carter and Steele (1982b) was the only study of lobster stomach contents to have measured prey availability. However, sea urchins were conspicuously abundant in each of the study areas. In the Elner and Campbell study, sea urchins were the most abundant macrofaunal species in the barrens (R. W. Elner, pers. comm.); and G. P. Ennis (Department of Fisheries and Oceans, St. John's, Nfld. A1C 5X1, pers. comm.) remembers them as one of the most if not the most abundant macrofaunal species in his study area. D. J. Scarratt (Biological Station, St. Andrews, N.B. E0G 2X0, pers. comm.) recalls urchins as being abundant, and Carter and Steele (1982b) listed urchins as the most abundant hard-bodied prey.

The additional references included above support the conclusion that urchins are unimportant prey of lobsters.

Breen states that I reported the results of his feeding studies (Breen 1974) incorrectly; I disagree. As described in his Comment, he offered lobsters five prey species, two at a time. The mean predation (kill) rate on urchins when offered with all other prey was 2.5% body weight·d^{-1}, not 0.4%·day^{-1} as shown in my table 1. However, table 1 clearly stated that the 0.4%·d^{-1} was only the predation rate on urchins offered in combination with green crabs. This single comparison was chosen because the green crab was a desirable prey and, as mentioned in the Perspective, a choice between sea urchins and undesirable prey would not be a fair measure of lobster predation on urchins. Horse mussels and periwinkles were eaten at $<10\%$ of the rate of green crabs, probably because only large individuals of these heavy shelled molluscs were offered. Predation on sea stars was an intermediate 30% of the rate on green crabs, so including urchin predation when offered with sea stars is a debatable choice. In the Perspective, predation rates on urchins in the presence of rock crabs (Evans and Mann 1977), blue mussels (Elner 1980), and green crabs (Breen 1974) at 0.5, 0.3, and 0.4% body weight·d^{-1}, respectively, were used. If the predation rates in the presence of sea stars (3.7%) were averaged with the other three values, after adjustment for seasonal variation, lobster predation rate on urchins is increased from 0.7 to 2.2 g·g $lobster^{-1}\cdot yr^{-1}$. This new value is close to 1.6 g urchin·g $lobster^{-1}\cdot yr^{-1}$, derived by another method, field stomach analysis, and would not change the conclusion that lobsters are responsible for only a minor portion of urchin mortality.

Breen also disagrees with my use of his thesis data on lobster feeding rates when urchins were the only prey choice. The rate he quotes was calculated from an equation relating feeding rate to prey density and temperature. To reduce the number of assumptions inherent in his calculation, I used instead his regressions of feeding rates on temperature at each of two prey densities (Breen 1974, p. 161–162).

Breen's fourth paragraph argues that my calculations of lobster predatory impact are too simple and that "The known complexity and the wealth of existing data dictate the use of some kind of model . . . ." He advises that this model should include densities and size distributions of each of lobsters, sea urchins, and other prey species; selectivity among prey; population dynamics of predators and prey; the effects of temperature, lobster size, and prey availability on predation rate; and complex behavioural interactions. Such models are capable of "demonstrating that an outcome of interest is impossible." Such a model would require more than 30 parameters, many of which would have not been measured or could not with confidence be extrapolated to the field. By adjusting parameter values entirely within reasonable ranges, the model could demonstrate anything whatsoever the modeller wanted it to demonstrate.

As with most exchanges of letters to journal editors, the reader is left to draw his own conclusions. However, a note of caution: the literature on the role of sea urchins in community dynamics is large, confusing, and includes work of good and not so good quality. If the reader is successful in assimilating this literature, it will surely give him a headache.

I thank Dr. R. W. Elner for commenting on this reply.—R. J. Miller, *Department of Fisheries and Oceans, P.O. Box 550, Halifax, N.S. B3J2S7.* (J9319)

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